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## DEVONIAN AND MISSISSIPPIAN CONULARIIDS OF NORTH AMERICA. PART A. GENERAL DESCRIPTION AND *CONULARIA*

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### ABSTRACT

The systematics, morphology and paleoecology of the new phylum Conulariida proposed here, from the Devonian and Mississippian rocks of North America are reviewed in this two-part work. Conulariids are identified by an elongate, pyramidal exoskeleton comprising a framework of calcium phosphate rods, with or without spines and nodes, covered by an integument made of thin layers of calcium phosphate and protein. Conulariids were gregarious invertebrate animals that were attached to substrata by means of calcium phosphate or chitinous stalks. These animals were exclusively marine and limited to rocks of the Ordovician through the Triassic. Conulariids are found in all types of marine facies and most probably had either a pseudoplanktonic or a benthonic lifestyle.

Three valid genera of conulariids are recognized in the Devonian and Mississippian of North America. These are *Conularia* Miller in Sowerby, 1821, *Paraconularia* Sinclair, 1940a and *Reticulaconularia* Babcock and Feldmann, n. gen. The genus *Diconularia* Sinclair, 1952 is considered to be a junior synonym of *Conularia*. Prior to 1986, 69 species-level taxa of conulariids were described from the Devonian and Mississippian of North America. Herein, and in Part B, 28 species are recognized as valid. Eleven species are assigned to *Conularia* and are described in Part A.

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## INTRODUCTION

Conulariids, members of an extinct phylum of invertebrates, have been described in the literature for a span of nearly 200 years. In that time, well over 400 species, subspecies or varieties, and over 40 genera have been named.

The purpose of this paper, and Part B of the same work, is to present taxonomic and morphologic information obtained from an examination of conulariids from Devonian and Mississippian strata of North America. Approximately 12% of all species-level conulariid taxa have been described based upon specimens collected from these rocks. Specimens described herein were collected only from the United States and Canada; conulariids are not known to have been collected in Mexico. This work involves: 1, studies of intraspecific and interspecific variation in morphology, ideally based upon large numbers of specimens; 2, studies of the stratigraphic and geographic distributions of species; and 3, analyses of conulariid anatomy, functional morphology and paleoecology, as the fossil record permits. Each taxon identified from Devonian or Mississippian rocks of North America is accompanied by a new, or in some cases, the first, illustration, and a description highlighting points of morphology now considered of greatest taxonomic value.

In the course of examining the Devonian and Mississippian forms, it became clear that it was necessary to revise the terminology related to morphology. In so doing, it was considered essential that conulariids from a much wider range of geological and stratigraphical occurrences had to be examined than those treated systematically herein. Thus, the detailed morphology and terms are intended to be applicable to all organisms referable to the Conulariida.

Part A of this work comprises a general description of the hard- and soft-part morphology of conulariids, occurrences and paleoecology of Devonian and Mississippian taxa of North America, a summary of the taxa treated both in this paper and in Part B, a key to the Devonian and Mississippian conulariid taxa of North America, and descriptions of species of that group which are referred to the genus *Conularia*. Part B of this work contains descriptions of species referable to the genera *Paraconularia* and *Reticulaconularia* n. gen. and specimens described in the literature as conulariids but which are here rejected from the phylum. Locality descriptions and measurements of selected specimens are included as appendices to Part B. Figures are numbered consecutively in both Parts A and B in order to avoid cross-reference confusion.

## MORPHOLOGY

*General.*—When preserved in three dimensions, the exoskeleton of a conulariid generally has a four sided, bilaterally symmetrical, elongate

pyramidal shape (Fig. 1.1). The profile may be modified by the development of one or more exoskeletal constrictions (Fig. 1.1). The exoskeleton, as preserved, generally ranges from 2 to 10 cm in length in full grown individuals. In a few species, however, the exoskeleton may attain a length in excess of 20 cm (Fletcher, 1938; Lamont, 1946; Sinclair, 1948; herein, Fig. 11.2). In nearly all instances, the conulariid exoskeleton diverges in width gradually and uniformly from a closed apical end to an open apertural end. The apical end may be closed either by a (morphological) apex (Fig. 1.1) or by an apical wall (Fig. 1.2). Presumed soft-parts consist of a single tubular structure that runs internally along the length of the exoskeleton and at least one globular body (Fig. 2.1).

*Morphologic terms.*—The literature on conulariid morphology includes important review papers by Slater (1907), Bouček and Ulrich (1929), Kiderlen (1937), Richardson (1942), Sinclair (1948, 1952), Moore and Harrington (1956*a*, 1956*b*) and Babcock and Feldmann (1986). Much misunderstanding of conulariid morphology has arisen from terms that have been improperly defined or undefined, from terms that are ambiguous and from terms that imply systematic affinities. Babcock and Feldmann (1986) proposed a set of morphological terms for conulariids that described morphological features without introducing unnecessary connotations of genetic affinities. Below is a list of morphological terms applied to conulariids, modified from Babcock and Feldmann (1986), together with terms here considered synonymous and which relate to the morphology of members of the phylum but are inappropriate in the light of advances made during this study.

**ADAPERTURAL SPINE**—long spine projecting from near the adapertural side of a rod, in the direction of the aperture.

**ADAPICAL SPINE**—short spine projecting from near the internal adapical side of a rod, in the direction of the apex.

**ALIMENTARY TRACT**—narrow, elongate, essentially tubular soft-part structure running the length of the central cavity. Synonyms: axial element, intestine.

**ANGULATED CIRCULAR CURVE**—style of rod articulation in which two abutting rods on a face form a broad arcuate, adapically concave ridge, interrupted by a slight adapertural point at the midline, and by gentle adapertural turns in the vicinity of the facial margins.

**APERTURAL CONSTRICTION**—exoskeletal constriction located nearest the aperture. Synonym: wrinkle.

**APERTURE**—opening at widest end of exoskeleton. Synonyms: base, mouth, opening.

**APERTURAL TERMINATION**—rounded or bluntly subtriangular extension of exoskeleton on each face at widest end of exoskeleton.

**APEX (MORPHOLOGICAL APEX)**—narrowest termination of exoskeleton, where the four faces join at a closed point. Synonyms: (biological) apex, summit. Compare with *hypothetical apex*.

**APICAL ANGLE**—hypothetical angle formed by one face of the exoskeleton; measured at the intersection of two lines each identified by tracing positions on the exoskeleton

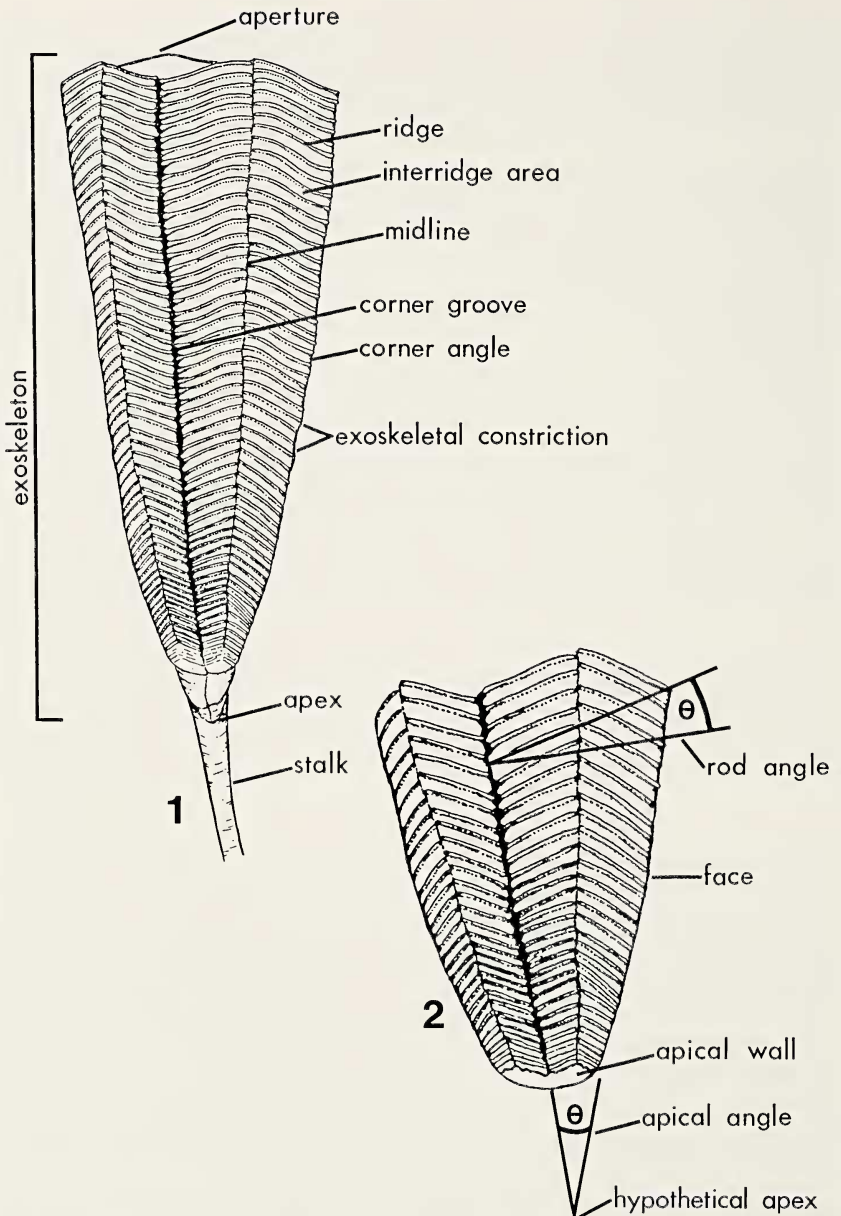


Fig. 1.—Conulariid morphology, exhibited by a generalized *Paraconularia*. 1.1; exoskeleton with stalk attached. 1.2; apical region with stalk removed. Morphological terms are explained in the text.

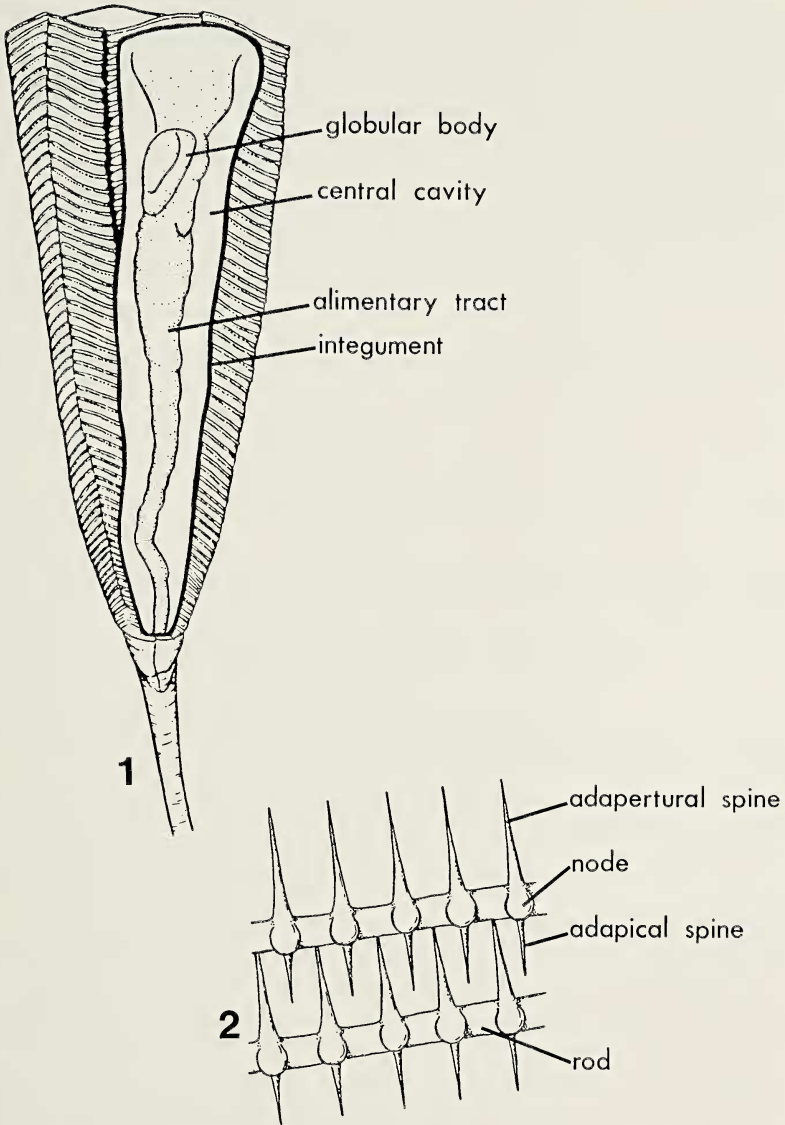


Fig. 2.—Conulariid morphology, exhibited by a generalized *Paraconularia*. 2.1; cutaway view of exoskeleton showing internal soft-parts. Structure of the soft-parts in the apertural region is problematic. 2.2; detailed view of two rods. Morphological terms are explained in the text.

- tangential to the facial margins and defining the maximum angle of separation. Synonym: facial angle. See *major apical angle* and *minor apical angle*.
- APICAL WALL**—broadly rounded, adapically convex, portion of integument lacking rods which completely covers the apical end of the exoskeleton when the apex itself is missing. Synonyms: apical septum, apical diaphragm, basal limitation, diaphragm, internal partition, *Schott*, septum.
- CENTRAL CAVITY**—region located internal to the four faces of the exoskeleton. Synonym: body cavity.
- CORNER ANGLE**—longitudinal line in the marginal region of a face connecting points of greatest inflection of the rods. Synonym: shoulder.
- CORNER GROOVE**—longitudinal invagination of exoskeleton connecting points where pairs of rods from adjacent faces cross near the marginal terminations of those rods. Synonyms: angular furrow, articulating suture, edge, lateral channel, longitudinal channel, marginal furrow, marginal groove, side furrow.
- EXOSKELETAL CONSTRICTION**—depression, restricted in the longitudinal direction, traceable on all four faces of the exoskeleton in the same relative position. Compare with *apertural constriction*.
- EXOSKELETON (SKELETON)**—four sided pyramidal structure, open at the widest end and closed at the narrowest end, comprising rods joined by integument. Synonyms: periderm, pyramid, shell, test.
- FACE**—one of four sides of the exoskeleton crossed by ridges; it is delimited by the aperture, by the apex or the apertural wall and by two corner grooves. Synonyms: side, surface, wall. See *major face* and *minor face*.
- GLOBULAR BODY**—large internal soft-part structure, subovoid in outline, located near the aperture. Synonym: esophagus.
- GOTHIC ARCH**—style of rod articulation in which two adjacent rods on a face form ridges that meet at an obtuse, adapically concave angle at the midline and proceed away from the midline along lines subtly curved adapically.
- HYPOTHETICAL APEX**—point in space where two lines, traced along the mean direction of the corner angles; meet; the hypothetical apex may or may not coincide with the position of the (morphological) apex.
- INFLECTED CIRCULAR CURVE**—style of rod articulation in which two adjacent rods on a face form a broadly arcuate, adapically concave ridge except in the vicinity of the facial margins, where they turn gently adaperturally.
- INFLECTED GOTHIC ARCH**—style of rod articulation in which two adjacent rods on a face form ridges that meet at an obtuse, adapically concave angle at the midline and proceed away from the midline along lines subtly curved adapically except in the vicinity of the facial margins, where they turn gently adaperturally.
- INTEGUMENT**—multilayered, presumably flexible, structure composed of calcium phosphate and protein, within which rods and spines were embedded and held in position. Synonyms: periderm, test.
- INTERRIDGE AREA**—roughly transverse band of integument located between two facial ridges. Synonyms: intercostal space, interspace, transverse furrow, transverse sulcus, space.
- INTERRIDGE CREST**—raised area, usually a linear ridge, located in an interridge area and positioned at a right angle to a ridge; formed by integument covering an adapertural or adapical spine. Synonyms: bar, intercostal longitudinal striation, vertical striation, longitudinal bar, longitudinal striation.
- INTERRIDGE FURROW**—low area, usually linear, located in an interridge area, and between two interridge crests.
- INTERROD AREA**—open region located between two rods; exposed only when integument is absent.
- MAJOR APICAL ANGLE**—apical angle subtended by a major face.

**MAJOR FACE**--wider of two adjacent faces.

**MARGIN (FACIAL MARGIN)**—longitudinal edge of a face, or a line connecting points where two faces meet in a corner groove.

**MIDLINE**—longitudinal line connecting points where either two adjacent rods on a face meet, or central to the facial terminations of each pair of adjacent rods if the rods do not meet. The midline can be expressed as either a thin groove or a raised line if the integument is preserved. The midline seems to be pigmented in some specimens. Synonyms: central face furrow, central facial groove, facial groove, facial midline, longitudinal carina, median groove, median line, mesial furrow, mid-line, middle line, parietal line, septum, structural channel.

**MINOR APICAL ANGLE**—apical angle subtended by a minor face.

**MINOR FACE**—narrower of two adjacent faces.

**NODE**—minute, subcircular, raised surface on a rod or ridge. Synonyms: granule, papilla, tubercle, pustule, wart.

**RIDGE (FACIAL RIDGE)**—raised line crossing a face from a corner groove to the midline area, and formed by integument covering a rod. Synonyms: costa, crenulation, ornamental rib, plica, plication, rib, riblet, transverse line, transverse rib, transverse ridge, transverse striation.

**ROD**—narrow, elongate structure that is subcircular in cross section, composed of calcium phosphate, and embedded within the integument; it is thickened near the marginal termination, and tapers very gradually to a blunt point at the facial termination.

**ROD ANGLE**—angle subtended by a line connecting the two most distant points of a rod along a longitudinal line and a line constructed perpendicular to the facial margin at the point where that ridge intersects the corner angle. Synonym: angle at the midline.

**ROD PAIR**—two rods on a face whose distal ends meet, or approach closely, at the midline.

**SKELETON**—See *exoskeleton*.

**SPINE**—solid, narrow, short or elongate structure, projecting from, and whose axis is at a right angle to, a rod; tapers gradually to a sharp point distally. See *adapical spine* and *adapertural spine*.

**STALK**—elongate structure, possibly chitinous, phosphatic, or chitinophosphatic, which articulates proximally with a conulariid apex; distally, the structure seems to attach to a substratum of uncertain nature.

*Abandoned morphological terms.*—The following terms, previously used in connection with the description of conulariids, are here considered inappropriate for various reasons including: 1, the structures have been shown to be taphonomic in origin; 2, the structures were described from organisms which should be excluded from the phylum Conulariida; 3, the structures have been shown to be absent in conulariids; or 4, the structures were described from dubious fossil material.

ANUS.

APPENDIX.

APERTURAL LOBE. Synonyms: apertural flap, apertural lip, flap, laterales, lobe, lip, mouth flap.

ATTACHMENT DISC.

BODY WALL.

EYE LENS.

HINGE.

FEATHER EDGE.

KEEL.

LATERAL LINE. Synonym: longitudinal line, line near midline.

MOUTH PANEL.

NERVE CENTER.

NET-SHAPED EPITHELIUM.

ORNAMENTATION. Synonym: sculpture.

PLATE. Synonym: transverse plate.

SEPTUM. Synonyms: carina, internal longitudinal rib, internal rib, internal rod, internal septum, longitudinal septum.

SKIN-MUSCLE LINING.

URULA.

WALL OPENING.

*Aperture.*—The aperture (Fig. 1.1) appears to have been a simple opening at the larger termination of the pyramidal exoskeleton. This region has been the subject of much speculation. “Flaps” or “lappets,” partially or wholly closing the apertural region, were first described by Miller (*in* Sowerby, 1821), and subsequently by Etheridge (1901), Laceron (1912), Richter and Richter (1930), Reed (1933), Kowalski (1935), Kiderlen (1937), Sinclair (1948), Moore and Harrington (1956*b*), Bransisa (1965) and others. Kiderlen (1937), Termier and Termier (1949) and Moore and Harrington (1956*b*) proposed elaborate mechanisms for closure of the apertural region involving the infolding of a flexible exoskeleton. They assumed the line of flexure to be a straight line normal to the midline. In one mechanism of closure, the exoskeleton not only folded along a straight line perpendicular to a face, but also collapsed like a bellows in the vicinity of the corner angles (Moore and Harrington, 1956*b*, Fig. 43.1). Moore and Harrington (1956*b*, p. F57) suggested that, in order for a conulariid to have been so flexible in the apertural region, the line of flexure at the base of each “apertural flap” was chitinophosphatic, while the remainder of the exoskeleton was phosphatic. No chemical data were presented in support of this hypothesis.

Specimens exhibiting closed or partially restricted apertures are common. Over 200 such specimens were observed in the course of this study (for example, Figures 8.1, 10.1, 28.2). Among these, there is no evidence of a consistent line of flexure (for example, Fig. 7.1–7.2, 8.7–8.9, 10.2, 18.2, 22.2–22.3). Typically, the line along which a flap is developed is not straight. Instead, the line of flexure often mimics the style of rod articulation or seems to be arbitrary. No two adjacent faces on the same specimen necessarily fold inward at the same position. Within the same species, there is no consistency from individual to individual either in the placement of a line of flexure or in the mode of closure, as defined by Kiderlen (1937), Termier and Termier (1949) or Moore and Harrington (1956*b*). Furthermore, “apertural flaps” have



been observed at multiple sites on single conulariid exoskeletons (Babcock and Feldmann, 1986, fig. 1E). Their presence at various places on the exoskeleton of different specimens indicates that they are taphonomic phenomena. Richter and Richter (1930), noted the extreme flexibility of the holotype of *Conularia tulipa* from the Hünsruckshiefer (Lower Devonian) of Germany. In their opinion, the conulariid exoskeleton was flexible enough to have collapsed under its own weight. Infoldings of exoskeleton commonly found in the apertural region, and less commonly elsewhere on a conulariid, are probably taphonomic structures resulting from collapse of the exoskeleton after death. The exoskeleton may not be quite as weak as suggested by Richter and Richter, but it is certainly not as rigid as a mollusk shell.

*Apex.*—The apical end of a conulariid may be: 1, a narrow, blunt point (Fig. 1.1); 2, truncated (Fig. 7.6); or 3, truncated, but having the end covered by a smooth, convex, imperforate apical wall (Fig. 1.2). The apex of a conulariid has been interpreted as a sharp point, as a bluntly rounded structure, as a smooth, imperforate wall, or as a smooth wall with a centrally located hole. Since the work of Kiderlen (1937), conulariids have been thought of as metazoans having a sharp point in the juvenile state. Presumably, the point was attached by an attachment disc to a hard substratum. Support for Kiderlen's argument was provided by supposed conulariids which were previously described by Ruedemann (1896*a*, 1896*b*). The specimens described by Ruedemann seem to be tubes of *Sphenothallus* (Feldmann et al., 1986). *Sphenothallus* has recently been shown to be unrelated to conulariids (Mason and Yochelson, 1985).

Apices of conulariids are exceedingly rare. The apices are not pointed as once interpreted, but are slightly rounded (Figs. 7.6, 16.6, 33.1–33.2). During life, most or all conulariids were attached by an elongate stalk (Figs. 1.1, 24.1–24.2, 32.5) to some substratum, during at least part of the life cycle. The apex was sheathed by the proximal portion of the stalk. Breakage at the proximal end of the stalk may possibly explain why so few conulariids are observed that have their apices intact.

Authentic conulariids with attachment discs have never been described. Small, round, black, and presumably chitinous or chitino-phosphatic, bodies attached to bryozoans or brachiopods have been identified in various museum collections as conulariid attachment discs. Often, the presumed base of a tube is preserved connected to such a structure. Such tubes are circular or subcircular in cross section. These problematic fossils probably represent attachment devices of some type of organism, but a relationship to conulariids has not been demonstrated.

Smooth, imperforate apical walls have been noted by many authors

(Miller *in* Sowerby, 1821; Hall, 1876, 1879; Slater, 1907; Richter and Richter, 1930; Sinclair, 1948; Moore and Harrington, 1956*b*; Babcock and Feldmann, 1984, 1986, herein, Figs. 4.1, 10.4, 11.2, 14.1, 14.4, 15.4, 19.1). These structures have been termed septa, apical diaphragms or *Schotten*. None of these terms seems appropriate, either because of its genetic implications or because of an incomplete description of the morphology. Apical walls are single units of integument that cover the convergent end of a conulariid close to the apical terminus. An apical wall is not located at the apical terminus itself, but seems to be attached to the interior of the faces on the exoskeleton, slightly adaperturally of this region. The line of juncture of the apical wall with the remainder of the integument always seems to occur near the narrowest portion of an exoskeletal constriction. Apical walls appear to lack support from rods or other structures, and may be bowed slightly in the adapical direction. Multiple apical walls may be present in single individuals (Eichwald, 1860; Steinmann and Doderlein, 1890; Slater, 1907; Sinclair, 1948).

References to conulariids with centrally perforated apical walls include Slater (1907), Richardson (1942), and Swartz and Richardson (1945). A collapsed specimen of *Conularia congregata* exhibiting a subcircular structure located centrally on the apical wall is illustrated in Figure 4.1. This subcircular structure is interpreted as having resulted from the compression of a thin, flexible apical wall against the apical portion of some soft-part morphologic feature such as the alimentary tract.

The function of the apical wall may have been to seal off the portion of the central cavity in which the conulariid lived from the stalk and older, unused portions of the body. In specimens preserving apical walls, the most apical portions of exoskeleton are not smooth (Figs. 11.2, 14.1). This indicates that conulariid exoskeletons like these may have been torn from their stalks by current forces. It is also possible that some few conulariids periodically may have shed unused portions of the exoskeleton (Babcock and Feldmann, 1984).

*Apical angle.*—An apical angle is measured at the intersection of two lines projected by tracing tangent lines along the trend of two adjacent corner grooves (Fig. 1.2). Apical angles are typically in the range of 8° to 26°.

The apical angle, as measured on a large segment of a specimen, may differ, by several degrees, from the apical angle as measured on a small section of the skeleton (see Appendix B in Part B). Small segments, particularly at exoskeletal constrictions and near the apex, usually yield somewhat larger apical angles than generalized apical angles, measured over a large segment of an exoskeleton.

A difference in the acute apical angle between adjacent sides of a

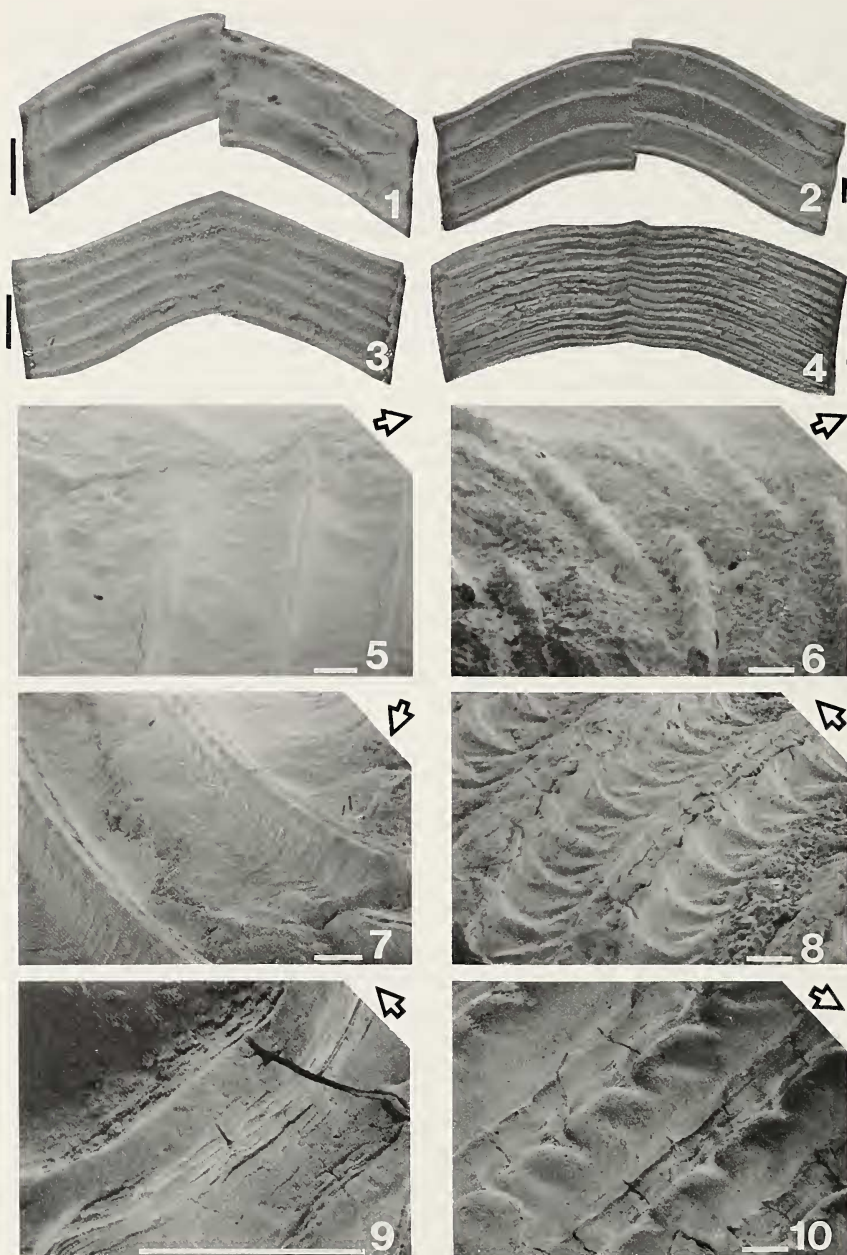
conulariid, mostly attributed to compression, has been noted by numerous authors, including Barrande (1867), Hall (1879), Slater (1907), Bouček (1939), and Sinclair (1948). Studies of compressed and presumably uncompressed materials indicate that opposite sides of a conulariid exoskeleton are paired (Babcock and Feldmann, 1984, 1986). In cross section, a conulariid is typically rectangular, if only slightly so (Figs. 30.4, 33.4). Each face subtends an apical angle equal to that of the face opposite it, but different from either adjacent face. This suggests that conulariids are bilaterally symmetrical, rather than tetramerally symmetrical, metazoans (Babcock and Feldmann, 1984, 1986). Rhomboid-shaped conulariids may exist, but most forms that are thought to have a rhomboidal cross section probably were described from subtly compressed specimens.

*Faces.*—In most cases, the four faces of the conulariid skeleton are essentially planar (Fig. 1.1). At least two forms, *Mesoconularia cahuanotensis*, from the Devonian of Bolivia (Branisa and Vanek, 1973) and *M. solitaria*, from the Silurian of Czechoslovakia (Sinclair, 1948), have faces that are markedly curved. In *Anaconularia anomala* from the Ordovician of Czechoslovakia, Kiderlen (1937) described a clockwise torsion of the exoskeleton, up to 40°. However, examination of eleven specimens referable to this taxon (GSC 85063–85073) indicates that these fossils, preserved in quartzite, are not twisted or compressed in a uniform fashion. Therefore, the “torsion” which Kiderlen observed may, in fact, be related to post-mortem diagenetic effects.

The two faces on a conulariid exoskeleton which subtend apical angles equal to each other, but smaller than the remaining two faces, are termed minor faces. Those two faces having larger apical angles are termed major faces.

*Integument.*—The thin walls, or faces, of the exoskeleton are made up of a multilayered calcium phosphate and protein integument (Ed Landing, personal communication, 1984; based upon electron microprobe analyses of specimens of *Paraconularia byblis* and *P. subulata* from locality 190). The precise number of layers and the extent to which this number is consistent from species to species has yet to be determined. In one example of *Conularia desiderata*, analyzed under the scanning electron microscope, at least thirty very thin, but discrete, layers of calcium phosphate were observed (Fig. 3.9). This stands in marked contrast to previous interpretations of the histology of the conulariid integument (for example, Sinclair, 1940*b*, 1948; Richardson, 1942), in which only two or three layers were observed through use of standard light microscopy.

*Rods.*—Rods (Fig. 2.2), embedded in the integument, are support structures which cross each face transversely; they are composed of calcium phosphate and are subcircular in cross section.



Each rod crosses one half of each face transversely until its distal end abuts with, or alternates with, the distal end of an adjacent rod. Proximally, rods of adjacent faces articulate in a corner groove. When covered by integument, a rod forms a thin ridge which traverses one half of each face of a conulariid skeleton.

A rod may be equipped with numerous spines (Fig. 2.2) which project adaperturnally or adaperturnally and adapically. When both types of spines are present, adaperturnal spines seem to be longer than adapical spines. The function of a spine was probably to provide a stronger framework to support the integument (Figs. 2.2, 3.8). Most conulariid species possess rods which have spines. Some, however, such as *Paraconularia planicostata* (for example, Fig. 3.1) and *P. subulata* (for example, Figs. 3.2, 3.6), have integument supported by rods alone.

Rods may or may not possess small nodes on the external side of the exoskeleton (Fig. 2.2). Nodes, if present, are arranged in a single row along a rod. These structures occur slightly adapically of each adaperturnal spine in all of the taxa reported herein (for example, Fig. 3.7). Thus, the number of adaperturnal spines and the number of nodes are equal. In *Paraconularia sorrocula*, the nodes seem to be fused with the adaperturnal spines, forming a single structure (Fig. 28.2).

The manner of rod articulation has long been used as a diagnostic character at the species level (Hall, 1859; Barrande, 1867; Holm, 1893). To delineate a "natural grouping" of the conulariids, Holm (1893) identified four species groups, based partially upon ridge characteristics. Richardson (1942) identified four modes of ridge arching among organisms which were then considered conulariids, presumably including

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Fig. 3.—3.1–3.4; rod articulation styles. 3.1; USNM 33785, *Paraconularia planicostata* (Dawson) showing gothic arch style; locality 165. 3.2; NYSM 3491, *P. subulata* (Hall) showing inflected circular curve style; locality 203. 3.3; AMNH 33018, *Conularia pyramidalis* Hall showing inflected gothic arch style; locality 117. 3.4; AMNH CU 282G, *C. elegantula* Meek showing angulated circular curve style; locality 174. 3.5–3.10; scanning electron micrographs; arrows point in apertural direction. 3.5; USNM 395833, *P. subulata* (Hall); view along midline showing integument draped loosely over rods; locality 190;. 3.6; USNM 395834, *P. subulata* (Hall), rods at midline, integument lacking; locality 72. 3.7; USNM 395830, *P. byblis* (White); integument closely draped over rods; locality 190. 3.8; USNM 395832, *C. desiderata* Hall, view of ridges, interridge crests and interridge furrows; rods have been broken away; locality 135. 3.9; USNM 395832, same specimen as in Fig. 3.8, *C. desiderata* Hall, ridge with rod removed, showing multilayered integument; locality 135. 3.10; USNM 395832, same specimen as in Fig. 3.8, *C. desiderata* Hall, view showing ridges with rods broken away, interridge crests and interridge furrows; locality 135. Bar scales equal 1 mm for Figs. 3.1–3.4 and 0.1 mm for Figs. 3.5–3.10.

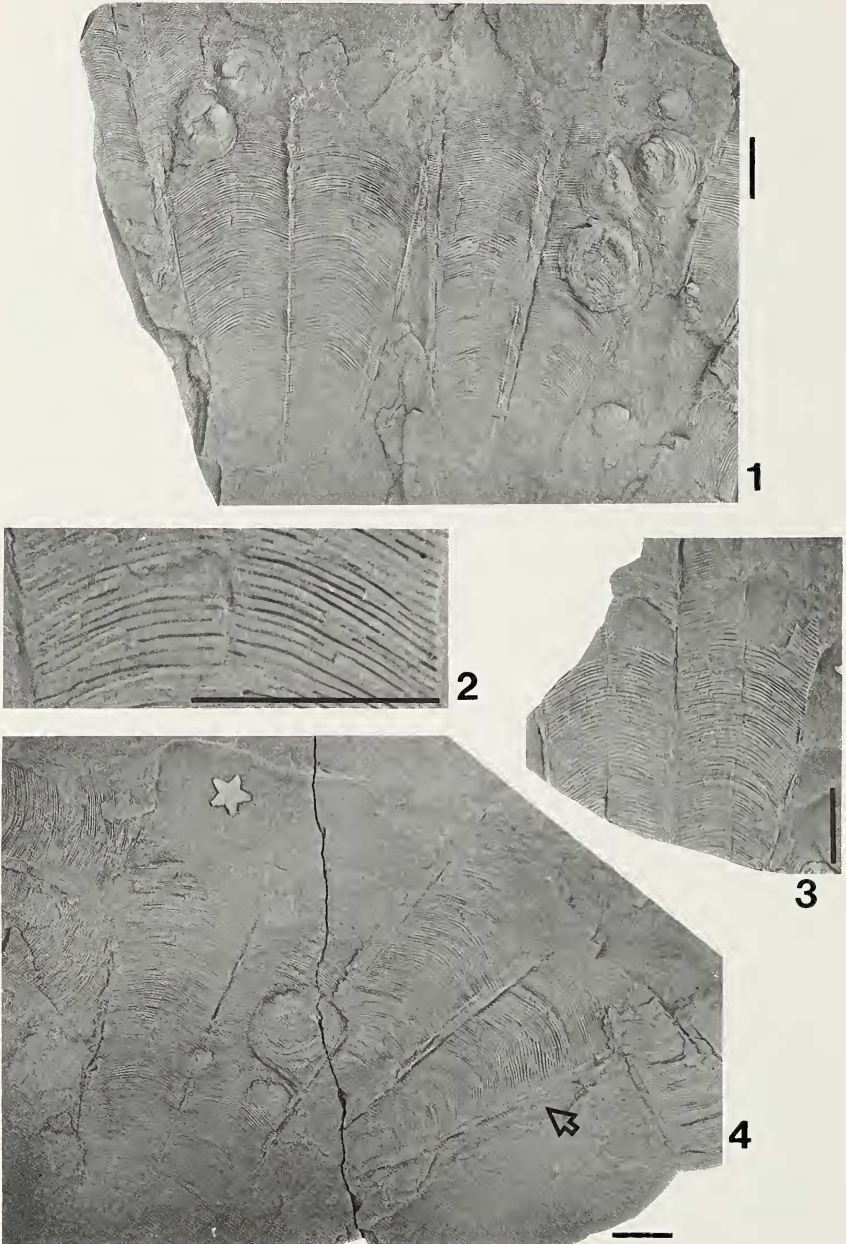


Fig. 4.—*Conularia congregata* Hall. 4.1; NYSM 3483, several paralectotypes from slab exhibiting lectotype and twelve paralectotypes, preserved in black shale. Note that shells

*Sphenothallus*, now considered a worm (Mason and Yochelson, 1985; Feldmann et al., 1986). Babcock and Feldmann (1986) recognized four modes of rod articulation which produce patterns of ridges useful as species-level taxonomic criteria. Their terminology for rod articulation patterns is followed herein; examples of each style are given in Figs. 3.1–3.4.

One additional feature of rod articulation at the midline is of interest for species-level determination of taxa. The two rods on a face which meet, or approach closely, at the midline are termed a rod pair. If the right rod of a rod pair is closest to the aperture when the specimen is examined with the aperture upward, the pattern of articulation is right superior (for example, Figs. 3.1, 3.2, 3.6). Conversely, if the left rod of a rod pair is closest to the aperture, the pattern is termed left superior (for example, Fig. 3.5). Some species can be distinguished from others, in part, by the relative proportions of right superior to left superior and to abutting rods on the major and minor faces.

An angle subtended by lines connecting the distal point of a rod with the point at which it joins the corner angle and a line projected across a face, perpendicular to the trend of the corner angle, from the point where a rod joins the corner angle, is termed a rod angle (Fig. 1.2). The description of a rod angle, combined with information on the style of rod articulation, is used herein as an effective way to help distinguish conulariid species. Rod angles generally vary across an exoskeleton within a few degrees. Notable changes in rod angles are often observed at the narrowest points of exoskeletal constrictions.

A complex of structures is produced on the external surface of the exoskeleton when the integument is draped over a framework of rods and spines. When integument covers a spine, an interridge crest is formed; when integument is draped between two adjacent spines, an interridge furrow is produced. A specimen preserved with the integument draped loosely over the rod and spine framework may appear to be of a different species than a specimen having integument diagenetically compressed close to the framework. It may also appear to be different from a specimen which lacks the integument altogether.

*Midline.*—A line, of variable distinctness, runs longitudinally down the middle of each face (Fig. 1.1). This line, termed the midline, may be a raised structure or a groove, and seems to be pigmented in some

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of the inarticulate brachiopod *Discina humilis* Hall are attached to the conulariid exoskeletons; locality 154. 4.2; NYSM 3484, detail of ridge structure as preserved in a counterpart specimen. 4.3; NYSM 3484, same specimen as in Fig. 4.2; locality 154. 4.4; NYSM 3483; lectotype and three paralectotypes exposed on same slab as specimens in Fig. 4.1; lectotype is indicated by an arrow. Bar scales represent 1 cm.

cases (Fig. 23.5). Wiman (1895), Knod (1908), and Liu (1981) have published hand-drawn figures of three separate structures radiating inward from the midlines of conulariids. Wiman (1895) described large T- or Y-shaped "septa," Liu (1981) figured elongate "septa" and Knod (1908) figured localized thickenings of integument. Among specimens examined from Devonian and Mississippian rocks of North America, there seems to be no evidence of an elongate, inwardly-directed structure associated with the midline. However, a thickening of the midline, on the internal side of the exoskeleton, has been observed on specimens of *Paraconularia ulrichana* from the Devonian of Bolivia. In some cases, there appears to be an invagination of the exoskeleton from the interior at the midline (Fig. 14.2).

*Corner groove.*—A corner groove (Fig. 1.1) is the facial invagination at a corner of the exoskeleton where two faces meet at right angles. An individual rod articulates proximally with an adjacent rod in a corner groove; rods on adjacent faces alternate in position along the corner groove. No evidence of localized thickenings of integument interior to the corner grooves, as described by Knod (1908), has been observed. The points of articulation of the rods in the corner grooves seem to be nodose swellings (Fig. 20.4).

*Exoskeletal constriction.*—An exoskeletal constriction (Fig. 1.1) is a slight depression in the conulariid exoskeleton which is identifiable at the same relative position on all faces. An exoskeletal constriction appears to be continuous about the four faces of the exoskeleton (for example, Figs. 5.3, 9.3–9.5, 10.1, 27.1–27.3). Trends of rod angles may change slightly (Figs. 8.3, 8.5), rods may converge (Figs. 8.5, 11.3) or an apical wall may be attached internally to the exoskeleton at the narrow end of such a structure (Figs. 11.2, 14.1). Exoskeletal constrictions may be indications that conulariids grew by the incremental addition of new integument and rods at the aperture. Because the apertural constriction, the last formed of the exoskeletal constrictions, is always located slightly adapically of the aperture (for example, Fig. 10.1), it is presumed that growth temporarily ceased near the widest portion of the exoskeleton, located between two adjacent exoskeletal constrictions.

"*Septa.*"—The term "septum" has been applied to three separate morphologic features in conulariids: 1, apical walls (for example, Miller in Sowerby, 1821; Slater, 1907); 2, ridges (Slater, 1907); and 3, T- or Y-shaped structures or unmodified elongate structures radiating inward from the faces at their midlines (Wiman, 1895; Kiderlen, 1897; Liu, 1981). None of these seems to be an appropriate application of the term. Most commonly, the word "septum" as applied to conulariids means large T- or Y-shaped structures of the exoskeleton that project inward from the midlines. These supposed hard-part structures were described in *Conularia loculata*, from the Silurian of Sweden by Wiman



(1895) and were thought by Kiderlen (1937) to be homologous to septa composed of endodermal tissue in living scyphomedusans. These structures have not been observed, at least not to such a marked extent, in any specimens other than those of Wiman. Wiman's material was illustrated only by drawings, and the specimens are now lost (W. A. Oliver, Jr., personal communication). Thus, Wiman's observations cannot be replicated.

The cross sectional view of a specimen of *Paraconularia subulata* illustrated in Fig. 33.4 exhibits a pattern of limonitic staining in the central cavity which roughly approximates Wiman's figures. The staining in this example is probably related to the preservation of incompletely decomposed internal viscera. It is suspected that Wiman and others may have been misled by some taphonomic feature such as this.

*Soft-part morphology.*—Much speculation has surrounded the study of the soft-parts of conulariids. Since the work of Kiderlen (1937), Knight (1937), Moore and Harrington (1956*a*, 1956*b*) and Werner (1966, 1967, 1969), conulariids have been interpreted as tentacled creatures. Support for such interpretation is weak, being based on a presumed homology of conulariids to medusoid cnidarians or upon a grouping of true medusoid cnidarians with the conulariids (Kiderlen, 1937; Knight, 1937; Moore and Harrington, 1956*a*, 1956*b*).

Remains of presumed conulariid soft-parts were independently described from European Devonian conulariids by Steul (1984) and from North American Mississippian conulariids by Babcock (1985*a*) and Babcock and Feldmann (1986). Babcock and Feldmann (1986), working only with exceptionally preserved three-dimensional specimens, identified a single elongate tube that extends the length of the central cavity and a large globular shaped structure near the aperture (Fig. 2.1). Steul's (1984) work, based upon x-ray analyses of collapsed specimens preserved in the Hunsrück Slate, revealed other structures which may be preserved soft-parts, though the evidence is ambiguous.

The tubular and globular internal structures (Figs. 30.2–30.6), presumably representing remains of organ systems, appear to be reduced in size compared to expected living organs and show no details of soft-part anatomy. These structures may be somewhat contracted masses of internal tissues. These structures may have been preserved, in outline at least, as altered remains of partially digested food matter and/or sediment left in the intestinal tract when the animals died. Other organs that were originally present in the North American studied specimens may have decayed.

#### OCCURRENCES AND PALEOECOLOGY

Conulariids have been reported exclusively from marine rocks ranging in age from the Late Precambrian to the Recent (Caster, 1957).

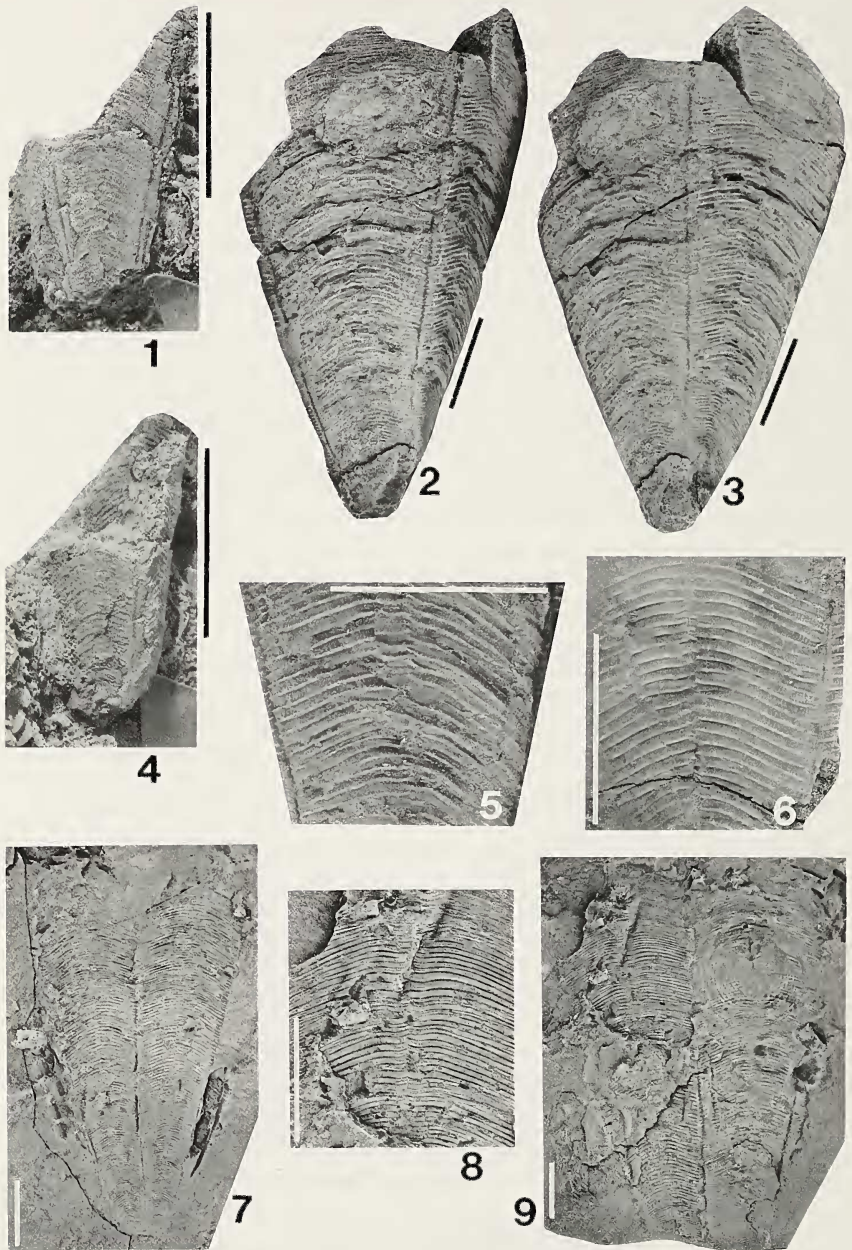


Fig. 5.—*Conularia desiderata* Hall. 5.1; AMNH 2697, holotype; major face, preserved in limestone; locality 121. 5.2; NYSM 3487, holotype of *C. continens* var. *rudis* Hall,

This range, however, includes a variety of taxa now referable to other groups. Occurrences here considered valid include specimens from Lower Ordovician (Sinclair, 1948) through Upper Triassic (Gou and Yang, 1985) rocks. While articulated conulariids are uncommon or rare in many instances, conulariids are, nonetheless, pervasive faunal elements in Middle Ordovician through Permian marine rocks. They are rare in the Lower Ordovician and in the Triassic. Some Paleozoic occurrences yield abundant conulariids.

Fossils identified as conulariids have been identified from all continents. However, the sole report of a conulariid from Antarctica (Cordini, 1955) has been received with skepticism and may represent plant material (Dalziel et al., 1981).

The conulariid skeleton, or exoskeleton, is composed of a calcium phosphate framework, made of rods, and usually having spines or nodes. The framework is set in an interlayered integument made of thin sheets of calcium phosphate and protein. Overall, the exoskeleton was probably fairly delicate, and upon death of the animal, was readily subject to collapse, occasional attachment of epibionts and decomposition accompanied by disarticulation (Feldmann and Babcock, 1986).

Most occurrences of articulated conulariids involve rapid burial and often, early diagenesis. For example, conulariids are abundant in the Meadville and Wooster members of the Cuyahoga Formation in northeastern and central Ohio. Specimens in these units are usually found in presumed tempestite beds or in siderite concretions. Specimens collected from tempestite beds often seem to be current aligned (Fig. 30.7). Specimens collected from siderite concretions, such as that illustrated in Fig. 10.4, are weakly current aligned, if at all. In the Cuyahoga Formation, concretions were probably produced through localized increases in pH and lowerings of eH, causing precipitation of iron carbonate. The onset of siderite precipitation probably occurred soon after burial of the animals.

Some occurrences of articulated conulariids involve "prefossilized" specimens, or ones which have undergone early diagenesis, and which have later been exhumed through bioturbation, winnowing of sediments by currents, or both. The specimens were later deposited in beds

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major face, preserved in siltstone; locality 132. 5.3; NYSM 3487, same specimen as in Fig. 5.2, corner view. 5.4; AMNH 2697, same specimen as in Fig. 5.1, minor face. 5.5; NYSM 3487, detail of minor face. 5.6; NYSM unnumbered, detail of specimen with integument draped loosely over rods; locality 124. 5.7; NYSM 3485, syntype of *C. continens* Hall, preserved in black shale. 5.8; NYSM 3486, syntype of *C. continens* Hall; detail of minor face; locality 125. 5.9; NYSM 3486, same specimen as in Fig. 5.8, nearly complete, flattened specimen. Bar scales represent 1 cm.

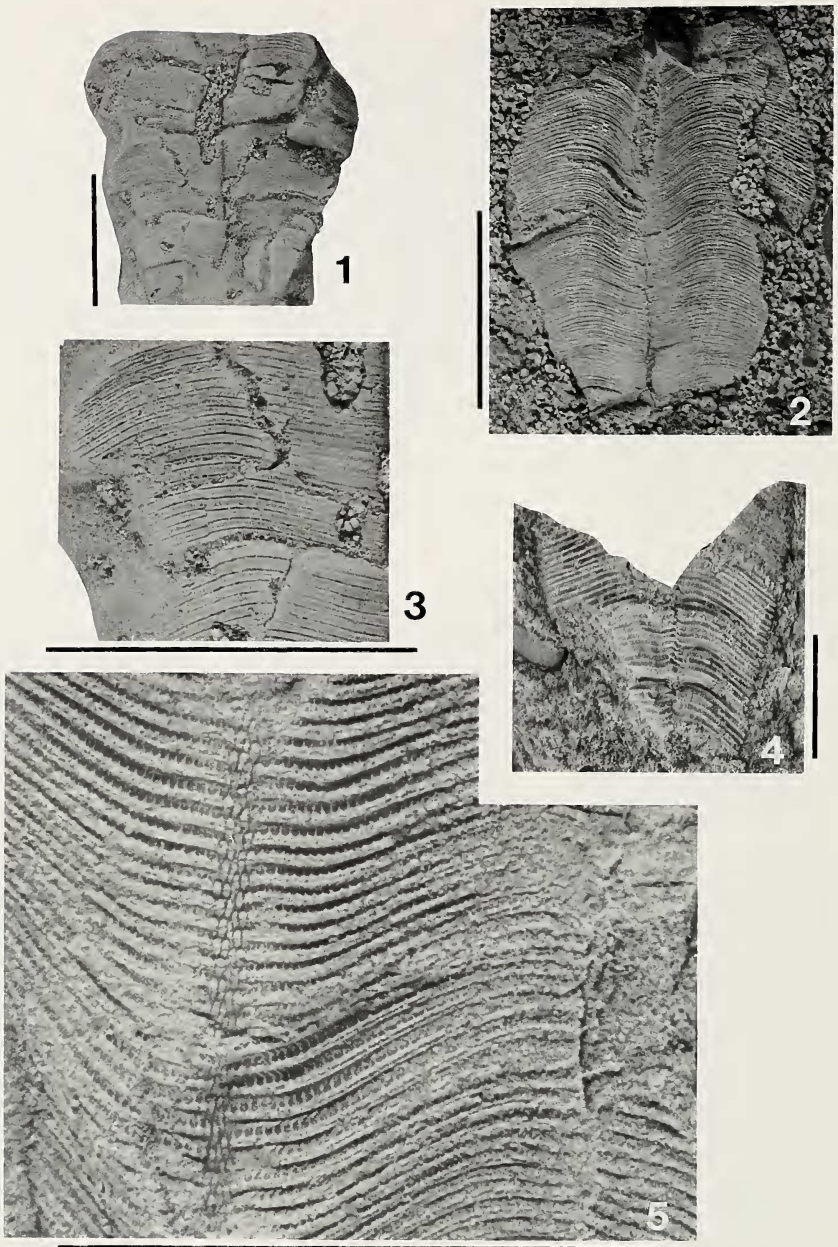


Fig. 6.—6.1–6.3; *Conularia delphiensis* (Maroney and Orr) preserved in phosphatic concretions at a stratigraphic discontinuity surface (Maroney and Orr, 1974). 6.1; IUPC

representing stratigraphic discontinuities (Maroney and Orr, 1974; Baird, 1981; Baird and Brett, 1981; herein, Figs. 6.1–6.3).

The general scarcity of articulated conulariid remains, at most localities, may be related to rapid disarticulation of the multielement skeleton, predation and scavenging, and the constancy of water movement near the sediment-water interface. The frequent occurrence of articulated conulariids in low diversity faunas (Ruedemann, 1934; Jux, 1960; Babcock and Feldmann, 1986; Feldmann and Babcock, 1986) may be largely a function of low biotic activity in these environments.

Many conulariids show indications that some breakdown of the exoskeleton has occurred, especially in the vicinity of the aperture (for example, Figs. 5.7, 7.5, 7.7), where the integument may be greatly reduced in thickness or lacking. In rare instances, poorly bioturbated stratigraphic units yield specimens of conulariids in which the integument is lacking over much of the exoskeleton and disarticulated rods have been displaced from their original positions (Fig. 21.4). In sediments that were probably well bioturbated, or sediments where water movement took place rather constantly, articulated conulariids are rare. It is possible that conulariid rods will be found in some Paleozoic and Mesozoic rock units that are sampled for microfossils by insoluble residue or other techniques. Disarticulated conulariid rods have been occasionally misidentified as fossil fish bones (Feldmann and Babcock, 1986).

Many species of conulariids seem to have been geographically widespread. For example, the Mississippian species, *Paraconularia chessterensis*, has a known geographic range from Alabama to British Columbia and, as with numerous other species, occurs in rocks of various lithologies. These lithologies include mudstones and wackestones (Chester Group of Illinois), gray shales (Borden Group of Indiana) and siderite concretions (Cuyahoga Formation of Ohio). The occurrence of this and other conulariid species in stratigraphic units of so vastly dissimilar lithologies and environments of deposition, and their wide geographic distribution, suggests that some species may have been planktonic or pseudoplanktonic at some point in the life cycle. The bilaterally symmetrical body plan (Babcock and Feldmann, 1984, 1986;

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14470-1, holotype; view of flattened specimen and detail of minor face; locality 23. 6.2; IUPC 14470-2, paratype; locality 23. 6.3; IUPC 14470-1, same specimen as in Fig. 6.1, detail of ?minor face. 6.4–6.5; *C. desiderata* Hall. 6.4; NYSM unnumbered, view of ?major face; locality 132. 6.5; USNM 395832, detail of specimen with most of integument removed, exposing broken rods and intact spines; locality 135. Bar scales in Figs. 6.1–6.4 represent 1 cm; bar scale in Fig. 6.5 represents 5 mm.

Steul, 1984), however, may be an indication that some species were weakly nektonic.

Conulariids are usually referred to as solitary animals. Clusters are rare, but a few have been figured by Slater (1907, Plate 2, fig. 1), Hall (1876, Plate 28, fig. 1; 1879 Plate 24, fig. 1), Sinclair (1944, Plate 2, fig. 5) and Babcock and Feldmann (1984, p. 17; Babcock and Feldmann, 1986, figs. 4A, 4C). In all these clusters, individual specimens are shown radiating about a central area. Apices are usually pointing inward in these aggregations (for example, Fig. 24.3). Occasionally, apices of such specimens are preserved intact (Fig. 24.1), yet in portions of a somewhat disaggregated cluster illustrated by Hall (1876, 1879), here illustrated in Figs. 4.1 and 4.4, the apices are missing, perhaps because of post-mortem decay. The apical walls are visible in some of these specimens.

A slab exhibiting numerous *P. chesterensis* from the Borden Group (Mississippian) of Indiana exhibits several small, black to reddish brown, tubular structures, circular in cross section, attached to, or very near the apices of, conulariids (Figs. 24.1, 24.3). Combined with discoveries of similar structures on conulariids from the Borden Formation (Mississippian) of Kentucky (Fig. 24.2) and from the Etherington Formation (Mississippian) of British Columbia (Fig. 32.5), these structures are interpreted as attachment stalks. The association of conulariids with plant remains, perhaps algae (for example, Fig. 28.7), indicates that some conulariids may have been pseudoplanktonic and were attached to, or entwined with, planktonic algae. Alternatively, the conulariids may have attached to plant remains which had previously settled to the ocean floor.

Cluster associations involving numerous specimens, usually comprising single species, serve to indicate that some, if not all, conulariids were gregarious, at least during some part of the life cycle. No evidence of budding or any other asexual reproductive style exists.

Regardless of whether the conulariids were planktonic, pseudoplanktonic, benthonic, or even nektonic, attached or free swimming, the soft-part organs in the region of the aperture of the exoskeleton probably functioned for filter feeding. There is no evidence for aggressive food gathering behavior.

The style of growth in conulariids was incremental, with addition of rods and spines taking place at the aperture. Growth lines, such as those seen on mollusks and brachiopods are not present. Exoskeletal constrictions, in exactly the same relative positions on all four faces, are possible evidences of incremental growth. Additional evidence of incremental growth at the aperture comes from some specimens showing healed injuries (for example, Figs. 20.1, 29.5). Along the exoskeletal

constrictions of such examples, rods may be broken or the rod articulation patterns may be disrupted. This indicates two things: 1, that the positions of apertural terminations changed and correspond to the positions of apertural constrictions; and 2, that the apertural terminations were easily fragmented but healing could occur during a succeeding growth phase.

Development of multiple apical walls may also have been a function of an incremental growth pattern. When the internal cavity of an individual reached a certain volume, an apical wall was probably secreted adaperturally of the apical terminus. Apical walls are commonly preserved among specimens referable to the genus *Conularia* but are rarely found on specimens of *Paraconularia*. No specimens of *Reticulaconularia* have been observed with apical walls in place.

Epibionts on conulariids include orbiculoid brachiopods (Hall, 1876, 1879; Moore and Harrington, 1956a; Babcock and Feldmann, 1984, 1986; herein, Figs. 4.1, 4.4, 5.9, 13.1, 13.5, 16.4, 28.1–28.2), encrusting bryozoans (Finks, 1955; herein, Figs. 22.4–22.5) and edrioasteroid echinoderms (Barrande, 1867; Moore and Harrington, 1956a). Attachment of epizoans has been interpreted as either having occurred during the life of the conulariid (Finks, 1955; Moore and Harrington, 1956a) or as having occurred after the death of the conulariid (Baird, 1981; Babcock and Feldmann, 1986). In all the specimens examined in the course of this study, orbiculoids seem to have attached to the conulariids after they died and came to rest on the sediment surface. This is supported by the observation that orbiculoids are always found attached to only two faces of a conulariid (Figs. 4.1, 4.4). Presumably, these two faces were the only ones which projected above the sediment-water interface. A specimen is illustrated herein (Fig. 25.5) of a bryozoan encrusting a conulariid in the region of a corner groove. There is no sign of damage to the bryozoan on this specimen, indicating that encrustation by the bryozoan occurred after the death of the conulariid.

#### SYSTEMATIC PALEONTOLOGY

*Summary of taxa.*—A total of 69 trivial names have been applied to Devonian or Mississippian conulariids of North America prior to this paper. Of these, 54 taxa were published, and eight were described in unpublished manuscripts. Herein and in Part B, 28 species are recognized as valid, of which five are new. However, primary type specimens of 18 species were not available for study; therefore, the status of these taxa was not assessed fully. In Part B, one species is removed from the Conulariida. The conulariids described below and in Part B are divided among three genera, *Conularia*, *Paraconularia* and *Reticulaconularia*, n. gen. The genus *Diconularia* Sinclair, 1952 is regarded

as a junior synonym of *Conularia* Miller *in* Sowerby, 1821 and the genus *Adesmoconularia* Driscoll, 1963 is considered to be a junior synonym of *Paraconularia* Sinclair, 1940a.

The list below summarizes all described species-level taxa of conulariids from North American Devonian and Mississippian rocks and indicates the status of each trivial name as currently recognized. Taxa are arranged alphabetically according to their presently recognized status. Junior synonyms and previously used combinations of each taxon are listed below each valid name.

- Conularia congregata* Hall, 1876  
*Conularia delphiensis* (Maroney and Orr, 1974)  
*Ctenoconularia delphiensis* Maroney and Orr, 1974  
*Conularia desiderata* Hall, 1861  
*Conularia continens* Hall, 1876  
*Conularia continens* var. *rudis* Hall, 1879  
*Conularia elegantula* Meek, 1871  
*Conularia milwaukeensis* Cleland, 1911  
*Conularia congregata* var. *milwaukeensis* Cleland, 1911  
*Conularia multicostata* Meek and Worthen, 1865  
*Conularia micronema* Meek, 1871  
*Diconularia micronema* (Meek, 1871)  
*Mesoconularia mcfarlani* Sinclair, [1948] MS  
*Mesoconularia attica* Sinclair, [1948] MS  
*Conularia pyramidalis* Hall, 1859  
*Conularia huntiana* Hall, 1859  
*Conularia lata* Hall, 1859  
*Conularia subcarbonaria* Meek and Worthen, 1865  
*Conularia intertexta* Miller, 1894  
*Conularia spergenensis* Miller and Gurley, 1893  
*Conularia tuzoi* Clarke, 1907  
*Conularia desiderata* var. *tuzoi* Clarke, 1907  
*Conularia ulsterensis* Howell, 1942  
*Conularia undulata* Conrad, 1841  
*Conularia cayuga* Hall, 1876  
*Conularia crebistria* Hall, 1876  
*Paraconularia alternistriata* (Shimer, 1926)  
*Conularia alternistriata* Shimer, 1926  
*Paraconularia alpenensis* Babcock and Feldmann, n. sp.  
*Paraconularia blairi* (Miller and Gurley, 1893)  
*Conularia blairi* Miller and Gurley, 1893  
*Conularia sedaliensis* Miller and Gurley, 1896  
*Paraconularia indiana* Sinclair, [1948] MS  
*Paraconularia byblis* (White, 1862)  
*Adesmoconularia byblis* (White), 1862  
*Conularia byblis* White, 1862  
*Paraconularia chagrinenensis* Babcock and Feldmann, n. sp.  
*Paraconularia chesterensis* (Worthen, 1883)  
*Conularia chesterensis* Worthen, 1883  
*Paraconularia missouriensis* (Swallow, 1860)  
*Conularia missouriensis* Swallow, 1860



- Conularia gratiosa* Miller and Gurley, 1893  
*Conularia greenei* Miller and Gurley, 1896  
*Paraconularia sciotovillensis* Driscoll, 1963  
*Paraconularia oklahomaensis* Babcock and Feldmann, n. sp.  
*Paraconularia planicostata* (Dawson, 1868)  
*Conularia planicostata* Dawson, 1868  
*Paraconularia recurvatus* Babcock and Feldmann, n. sp.  
*Paraconularia salinensis* (Whiteaves, 1891)  
*Conularia salinensis* Whiteaves, 1891  
*Paraconularia sorrocula* (Beede, 1911)  
*Conularia sorrocula* Beede, 1911  
*Paraconularia subulata* (Hall, 1858)  
*Conularia subulata* Hall, 1858  
*Conularia victa* White, 1862  
*Conularia newberryi* Winchell, 1865  
*Conularia whitei* Meek and Worthen, 1865  
*Conularia sampsoni* Miller, 1892  
*Paraconularia wellsvillia* Babcock and Feldmann, n. sp.  
*Paraconularia yochelsoni* Babcock and Feldmann, n. sp.  
*Reticulaconularia penouili* (Clarke, 1907)  
*Conularia penouili* Clarke, 1907  
*Conularia gaspesia* Sinclair, 1942  
*Reticulaconularia sussexensis* (Herpers, 1949)  
*Conularia sussexensis* Herpers, 1949

#### *Whereabouts of Type Material Unknown*

- Climacoconus viata* Swartz and Richardson in Richardson, [1942] MS  
*Conularia crawfordsvillensis* Owen, 1862  
*Conularia gracilis* Herrick, 1888  
 (Name preoccupied by *C. gracile* Hall, 1847; changed to *C. herricki* by Miller, 1892.)  
*Conularia grandis* Roemer, 1856  
*Conularia herricki* Miller, 1892  
*Conularia jervisensis* Shimer, 1905  
*Conularia latooides* Swartz and Richardson in Richardson, [1942] MS  
*Conularia marionensis* Swallow, 1860  
*Conularia missouriensis* var. *hermansii* Calvin, 1890  
*Conularia molaris* White, 1876  
*Conularia novascotica* Hartt, in Dawson, 1868  
*Conularia osagensis* Swallow, 1863  
*Conularia pyramidalis* var. *parvinodis* Swartz and Richardson in Richardson, [1942] MS  
*Conularia siphunculophora* Swartz and Richardson in Richardson, [1942] MS  
*Conularia triplicata* Swallow, 1860  
*Conularia verneuilia* Emmons, 1846  
*Paraconularia welleri* Sinclair, [1948] MS

#### *Non-Conulariid*

- Conularia tenuicostata* Branson, 1938  
 (Assigned, tentatively, to phylum Priapulida.)

*Repositories.*—Specimens are listed according to catalogue numbers with the repositories abbreviated as follows:

AMNH	American Museum of Natural History, New York, New York
AMNH CU	American Museum of Natural History, Columbia University Collection, New York, New York
BMS	Buffalo Museum of Science, Buffalo, New York
CM	Carnegie Museum of Natural History, Invertebrate Paleontology Collections, Pittsburgh, Pennsylvania
CMNH	Cleveland Museum of Natural History, Invertebrate Paleontology Collections, Cleveland, Ohio
FMNH P	Field Museum of Natural History, Paleontology Collection, Chicago, Illinois
FMNH PE	Field Museum of Natural History, Invertebrate Paleontology Collection, Chicago, Illinois
FMNH UC	Field Museum of Natural History, University of Chicago Collection from Walker Museum, Chicago, Illinois
GSC	Geological Survey of Canada, Ottawa, Ontario
ISGS	Illinois State Geological Survey, Illinois State Museum, Champaign-Urbana, Illinois
IUPC	Indiana University Paleontological Collection, Bloomington, Indiana
KSU	Department of Geology, Kent State University, Kent, Ohio
NJSM	New Jersey State Museum, Trenton, New Jersey
NYSM	New York State Museum and Science Service, Albany, New York
OC	Oberlin College Paleontological Collections, Oberlin, Ohio
PU	Department of Geology, Princeton University, Princeton, New Jersey
RM(MU)	Redpath Museum (McGill University), Montreal, Quebec
UCGM	University of Cincinnati Geological Museum, Cincinnati, Ohio
UIPC	University of Illinois, Department of Geology, Champaign-Urbana, Illinois
UK	University of Kentucky, Department of Geology, Lexington, Kentucky
UMC	University of Missouri-Columbia, Columbia, Missouri
UMMP	University of Michigan, Museum of Paleontology, Ann Arbor, Michigan
USNM	United States National Museum of Natural History, Washington, D.C.
WVU	West Virginia University, Department of Geology, Morgantown, West Virginia

*Treatment of manuscript names.* — One of the most influential papers regarding the systematics and morphology of conulariids is Sinclair (1948), an unpublished Ph.D. thesis. In it were proposed many new genus-level and species-level taxa. The undescribed genera identified by Sinclair were subsequently published (Sinclair, 1952); however, the majority of Sinclair's new species have never been formally described. Moreover, many of the species removed by Sinclair from *Conularia*, as used in the sense of a form-genus, and placed in different genera, have not been published in their revised state by Sinclair. Nevertheless, various authors have used Sinclair's combinations, often without reference to the authority for such usage.

It is our opinion that, because of the central importance of Sinclair's (1948) unpublished manuscript to the study of conulariid systematics, Sinclair's unpublished species-level names and his unpublished combinations should be included in the formal synonymies of the Devonian and Mississippian taxa discussed below. For the sake of completeness,

we have also included in the present work the manuscript names of Swartz and Richardson *in* Richardson (1942). By including these unpublished names in synonymy though, we do not intend to suggest that these are available names. According to Article II(d)(ii) of the *International Code of Zoological Nomenclature, Third Edition* (International Commission of Zoological Nomenclature, 1985), "a previously unavailable name is not changed by its mere citation accompanied by a reference to the work in which the name was published but was not made available." Also, in Article 11(e), the *Code* states that a, "name first published as a junior synonym is not thereby made available unless prior to 1961 it has been treated as an available name . . ."

#### Phylum CONULARIIDA Babcock and Feldmann, new phylum

*Diagnosis.*—Animals generally possessing a four sided, steeply pyramidal exoskeleton; bilaterally symmetrical; integument composed of calcium phosphate and protein, multilayered, moderately flexible; exoskeletal framework composed of calcium phosphatic rods arranged transversely across each side face; adjacent rods abut or alternate at midline of each face; rods of adjacent faces articulate in a groove at junction of two faces; apical end closed either by a blunt point; one or more smooth apical walls may be present internal to the exoskeleton and apertured the apex; apex sheathed by a ?chitinous, phosphatic, or chitinophosphatic stalk; aperture simple and open. No internal hard-part structures known; internal soft-parts comprise an elongate tube extending most of the body length, in addition to one or more globular shaped structures, all of uncertain function.

*Remarks.*—Approximately 40 genera of organisms have, at one time or another, been grouped among the conulariids. Of these, six genera have been excluded from the phylum to date. Based upon new information on the architecture of the conulariid skeleton (Babcock and Feldmann, 1986), it seems that even more genera have been described than are warranted by fossil evidence. Upon further study, several other genera are likely to be excluded from the phylum Conulariida.

Organisms which are properly included within the phylum Conulariida must possess a bilaterally symmetrical exoskeleton composed of calcium phosphate rods and layered calcium phosphate and protein integument. Herein, genera of conulariids are defined upon: 1, the relative spacing of rods; 2, the relative proportion of rods that abut at the midline to those that alternate; 3, the apical angles; 4, the presence or absence of nodes and spines; and 5, the spacing of nodes and spines. Species are distinguished using the characters upon which generic distinctions are made as well as the following: 1, the patterns of rod articulation; and 2, the rod angles.

Descriptions of conulariids represented in the Devonian and Mississippian rocks of North America follow. After examination of specimens referred to the respective type species from Europe, Sinclair (1940a) proposed North American reference species. The following diagnoses of *Conularia* and *Paraconularia* are based largely upon specimens referable to the North American reference species. The new genus *Reticulaconularia* is based upon specimens from the Devonian of eastern North America.

Specimens of *Conularia* are recognizable by their closely spaced rods, by having more than 40% of the rods abutting at the midline, by having small apical angles and by having both nodes and spines which are closely spaced. Specimens referable to *Paraconularia* exhibit widely spaced rods, fewer than 40% of rods abutting at the midline and small apical angles. Nodes and spines may be present; if they are, they are closely spaced. Conulariids referable to *Reticulaconularia*, n. gen. have widely spaced rods which abut or alternate at the midline in proportions which are not well established yet. They also have large apical angles. Members of the genus *Reticulaconularia* are notable for the reticulate appearances of the external surfaces of the faces (Figs. 33.1–33.5, 34.1–34.2, 34.4), a product of nodes and spines which are widely spaced. It should be noted, however, that other conulariids, if preserved as external molds, may exhibit patterns similar to this “reticulate” appearance (for example, Figs. 8.5–8.6). Such specimens are best studied with latex casts.

*Key to North American Devonian and Mississippian conulariids.*—The following is a key to all species of Devonian and Mississippian conulariids from North America which are currently known. Some categories are ambiguous due to the lack of complete or well preserved specimens of some species, so it is not intended for use with specimens of different ages or of other areas of the world.

1. Faces have reticulate appearance ..... 2
1. Faces do not have reticulate appearance ..... 3
2. Inflected gothic arch rod articulation present .....  
..... *Reticulaconularia sussexensis* (Herpers)
2. Inflected gothic arch rod articulation not present .....  
..... *Reticulaconularia penoulli* (Clarke)
3. Number of rods that abut at midline less than 40% ..... 4
3. Number of rods that abut at midline greater than or equal to 40% ..... 19
4. Gothic arch rod articulation present ..... 5
4. Gothic arch rod articulation not present ..... 9
5. Only gothic arch rod articulation present .. *Paraconularia alternistriata* (Shimer)
5. Gothic arch and another style of rod articulation present ..... 6
6. Gothic arch and inflected circular curve rod articulation present .....  
..... *Paraconularia oklahomaensis* Babcock and Feldmann, n. sp.
6. Gothic arch and inflected gothic arch rod articulation present ..... 7

7. Rods/cm fewer than or equal to 11 ..... *Paraconularia planicostata* (Dawson)  
 7. Rods/cm greater than 11 ..... *Paraconularia yochelsoni* Babcock and Feldmann, n. sp.
8. Inflected gothic arch rod articulation present ..... 9  
 8. Inflected gothic arch rod articulation not present ..... 14
9. Only inflected gothic arch rod articulation present ..... 10  
 9. Inflected gothic arch and another style of rod articulation present ..... 11
10. Rods/cm fewer than 15 .....  
 ..... *Paraconularia chagrinensis* Babcock and Feldmann, n. sp.
10. Rods/cm greater than 15 ..... *Paraconularia sorrocula* (Beede)
11. Rods/cm fewer than or equal to 12 ..... 12  
 11. Rods/cm greater than 12 ..... 13
12. Rods are slightly inflected at midline .. *Paraconularia blairi* (Miller and Gurley)  
 12. Rods are not inflected at midline ..... *Paraconularia subulata* (Hall)
13. Number of rods that abut at midline fewer than 30% .....  
 ..... *Paraconularia salinensis* (Whiteaves)
13. Number of rods that abut at midline greater than or equal to 30% .....  
 ..... *Paraconularia byblis* (White)
14. Inflected circular curve rod articulation present; rods recurved near midline .. 15  
 14. Inflected circular curve rod articulation present; rods not recurved near midline  
 ..... *Paraconularia wellsvillia* Babcock and Feldmann, n. sp.
15. Rods/cm fewer than or equal to 12 ..... 17  
 15. Rods/cm greater than 12 ..... 16
16. Rods/cm fewer than 18 .. *Paraconularia alpenensis* Babcock and Feldmann, n. sp.  
 16. Rods/cm greater than or equal to 18 .....  
 ..... *Paraconularia recurvatus* Babcock and Feldmann, n. sp.
17. Rods/cm fewer than or equal to 7 ..... *Paraconularia chesterensis* (Worthen)  
 17. Rods/cm greater than 7 ..... *Paraconularia missouriensis* (Swallow)
18. Gothic arch rod articulation present ..... *Conularia pyramidalis* (Hall)  
 18. Gothic arch rod articulation not present ..... 19
19. Inflected gothic arch rod articulation present ..... 20  
 19. Inflected gothic arch rod articulation not present ..... 23
20. Rods/cm fewer than or equal to 30 ..... 21  
 20. Rods/cm greater than 30 ..... 22
21. Rods/cm fewer than or equal to 25 ..... *Conularia milwaukeensis* Cleland  
 21. Rods/cm greater than 25 ..... *Conularia multicostata* Meek and Worthen
22. Rods/cm fewer than or equal to 39 ..... *Conularia tuzoi* Clarke  
 22. Rods/cm greater than 39 ..... *Conularia ulsterensis* Howell
23. Angulated circular curve rod articulation present ..... 24  
 23. Angulated circular curve rod articulation not present ..... 27
24. Only angulated circular curve rod articulation present ..... 25  
 24. Angulated circular curve and another style of rod articulation present ..... 26
25. Rods/cm fewer than 34 ..... *Conularia subcarbonaria* Meek and Worthen  
 25. Rods/cm greater than 34 ..... *Conularia elegantula* Meek
26. Rod angle less than or equal to 17° ..... *Conularia congregata* Hall  
 26. Rod angle greater than 17° ..... *Conularia desiderata* Hall
27. Rods undulose ..... *Conularia undulata* Conrad  
 27. Rods not undulose ..... *Conularia delphiensis* (Maroney and Orr)

Genus *CONULARIA* Miller, in Sowerby, 1821

*Type species.*—*Conularia quadrisulcata* Sowerby, by original designation; Silurian of England. Holotype is lost. North American reference

species, *vide* Sinclair (1940a): *Conularia niagarensis* Hall, 1852 (Silurian). Syntypes and plastosyntypes of *C. niagarensis*: AMNH 31625–31628; plastosyntype of AMNH 31625: FMNH UC 60850.

*Diagnosis.*—Conulariids with rods that are generally closely spaced, 9–84 rods/cm. Fewer than 60% of rods alternate at midline; more than 40% abut; two adjacent rods on a face form a single arc across the face. Apical angles small, 9–23°. Nodes, adapertural spines and adapical spines usually present and closely spaced, 1–7/mm.

### *CONULARIA CONGREGATA* Hall, 1876

Figs. 4.1–4.4

*Conularia congregata* Hall, 1876, Pl. 28, fig. 1; Miller, 1877, p. 141; Bigsby, 1878, p. 418; Hall, 1879, p. 214–215, Pl. 34, fig. 1, Pl. 34A, figs. 9–11; Miller, 1889, p. 390; Harris, 1899, Pl. 8, fig. 59; Clarke and Ruedemann, 1903, p. 565; Moore and Harrington, 1956b, p. F61, fig. 46.2; Palmer and Brann, 1966, fig. 59; Babcock, 1985b, fig. 2; Babcock and Feldmann, 1986, fig. 4A.

*Conularia* s.l. *congregata* Hall. Sinclair, 1948, p. 286.

*Conularia pyramidalis* Hall. *Sensu* Babcock and Feldmann, 1984, p. 17.

*Description.*—Exoskeleton up to 11 cm in length. Major apical angle 17–18°; minor apical angle 12–14°. Rod articulation exclusively of inflected circular curve style. Rods almost always abut at midline; rod angle 9–13°. 16–21 rods/cm. 6–7 nodes/mm; 6–7 adapertural spines/mm; 6–7 adapical spines/mm; spines often not easily discernible. Apical wall may be present.

*Occurrences.*—Upper Devonian of New York; localities 149–150 and 152–160. Maillieux (1933), Markovski and Nalivken (1934) and Xu and Li (1979) reported *C. congregata* from Devonian rocks in Belgium, the U.S.S.R. and the People's Republic of China, respectively, but these occurrences have not been confirmed.

*Types.*—Lectotype and twelve paralectotypes on one slab, NYSM 3483. Remains of at least thirteen specimens are preserved on James Hall's slab of syntypes (Figs. 4.1, 4.4). From this syntypic suite, the best preserved of Hall's figured specimens (Fig. 4.4) is here chosen as the lectotype of *C. congregata*. The remaining ten specimens are considered paralectotypes. Counterparts of the paralectotype specimens shown in Fig. 4.1 are catalogued as FMNH unnumbered.

*Remarks.*—*Conularia congregata* Hall is most similar in morphology to *C. desiderata* Hall. The similarities lie in overall size, apical angle values, rod angle values and in the presence of inflected circular curve rod articulation. The differences between the two taxa are subtle. In specimens of *C. congregata*, few rods, generally fewer than 10%, alternate at the midline; also, rods show very little or no inflection toward the aperture near the midline. Among specimens referable to *C. desiderata*, as many as 15% of the rods may alternate at the midline; specimens also show a strong adapertural inflection of the rods at the

midline. Some specimens, such as that illustrated in Fig. 5.6, appear to be intermediate in morphology between *C. desiderata* and *C. congregata*.

*Conularia congregata* may also be confused with *C. pyramidalis* Hall. *Conularia pyramidalis* differs from both *C. congregata* and *C. desiderata* in having inflected circular curve rod articulation in the apical region and inflected gothic arch rod articulation elsewhere. There is no evidence in *C. pyramidalis* that the rods deflect near the midline.

*Material examined.*—40 specimens; housed in the AMNH, BMS, FMNH, NYSM, USNM, and the private collection of Paul Zell.

### **CONULARIA DELPHIENSIS** (Maroney and Orr, 1974)

Figs. 6.1–6.3

*Conularia* sp. Kindle, 1901, p. 737, Pl. 123, fig. 8.

*Ctenoconularia delphiensis* Maroney and Orr, 1974, p. 3–6, fig. 1A–F.

*Description.*—Exoskeleton up to 5.5 cm in length. Major apical angle and minor apical angle about 15°. Rod articulation inflected gothic arch style in apical region and inflected circular curve style elsewhere. Rods usually abut at midline; rod angle 10–11°. 26–42 rods/cm. 6–7 nodes/mm; adaperatural spines and adapical spines not observed. Apical wall not observed.

*Occurrence.*—Upper Devonian of Indiana; localities 22–23.

*Types.*—Holotype, IUPC 14470-1; five paratypes, IUPC 14470-2 through 14470-6.

*Remarks.*—The six specimens which comprise the type suite of *C. delphiensis* are badly preserved. Although no spines were actually observed on any of the type specimens, all other morphologic features are consistent with species of the genus *Conularia* as defined herein. A specimen figured by Kindle (1901, pl. 123, fig. 8; USNM 62210), an apparent external mold of *C. delphiensis*, clearly shows that nodes are present, but spines are not evident. Spines may have been present in this taxon, but have not been observed because of the poor preservation of the specimens studied. A cross sectional view of an un-compressed specimen referable to this species has not been observed.

In their original description of *C. delphiensis*, Maroney and Orr (1974) did not indicate why they chose to include the species in the genus *Ctenoconularia* Sinclair, 1952. Moreover, they only compared this species to *Conularia congregata*. Sinclair (1952, p. 141) noted that the primary distinguishing characteristic of specimens referable to *Ctenoconularia* was “strikingly slender shells.” This is certainly true in the type species, *Ctenoconularia obex* Sinclair. Judging from Sinclair’s published figures (1952, figs. 56 A–C), the major and minor faces subtend angles of 4° and 3°, respectively. In other respects, specimens of *Ctenoconularia* are very similar to specimens of *Conularia*. “*Cten-*

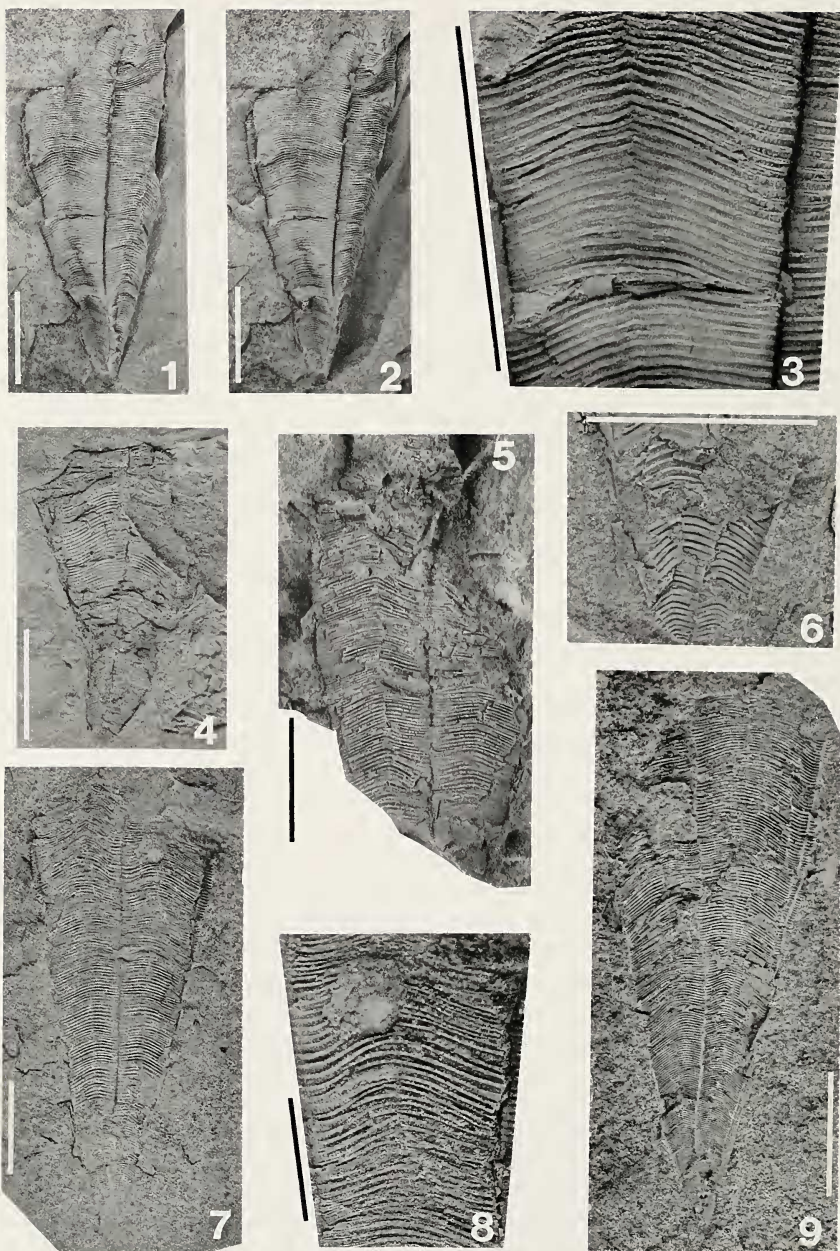


Fig. 7.—7.1–7.4; *Conularia elegantula* Meek. 7.1; AMNH CU 282G, holotype, corner view; locality 174. 7.2; AMNH CU 282G, same specimen as in Fig. 7.1, corner major



*conularia*" *delphiensis*, which has apical angles of approximately 15°, seems to expand from the apex too rapidly to warrant inclusion in the genus *Ctenoconularia*.

*Conularia delphiensis* is similar in general morphology, including similarity of rod articulation styles, to only one Devonian species from North America, *C. milwaukeeensis*. *Conularia delphiensis* differs, however, in having greater rods/cm values. Specimens here referred to *C. delphiensis* possess 26–42 rods/cm while specimens here referred to *C. milwaukeeensis* have fewer than 30 rods/cm.

*Material examined*.—8 specimens; housed in the IUPC and the USNM.

### **CONULARIA DESIDERATA** Hall, 1861

Figs. 3.8–3.10, 5.1–5.9, 6.4–6.5, 16.6

*Conularia*——? Hall, 1859, p. 480.

*Conularia desiderata* Hall, 1861, Pl. 72A, fig. 4; Richardson, 1942, p. 30–32, Pl. 4, figs. 7, 8; Babcock and Feldmann, 1986, figs. 1B, 1H.

*Conularia continens* Hall, 1876, Pl. 28, figs. 4–6; Miller, 1877, p. 141; Bigsby, 1878, p. 418; Hall, 1879, p. 212–214, Pl. 33, fig. 6, Pl. 34, figs. 3, 4, 6, Pl. 34A, fig. 6; Lesley, 1889, p. 143, fig.; Miller, 1889, p. 390; Clarke and Ruedemann, 1903, p. 565; Moore and Harrington, 1956a, fig. 25.1; Moore and Harrington, 1956b, p. F60, fig. 42.10a–b; Tasch, 1973, fig. 5.15H, Tasch, 1980, fig. 5.15H.

*Conularia continens* var. *rudis* Hall, 1879, p. 215–216, Pl. 34A, figs. 7–8; Miller, 1889, p. 390; Clarke and Ruedemann, 1903, p. 565; Grabau, 1906, p. 331.

*Conularia* s.l. *continens* Hall. Sinclair, 1948, p. 286.

*Paraconularia desiderata* (Hall). Sinclair, 1948, p. 185.

*Conularia* s.l. *rudis* Hall. Sinclair, 1948, p. 284.

*Description*.—Exoskeleton up to 10 cm in length. Major apical angle 14–27°; minor apical angle 14–18°. Rod articulation inflected circular curve in early stages to angulated circular curve in later stages. Rods almost always abut at midline; rod angle 7–17°. About 41 rods/cm in apical region; 14–27 rods/cm elsewhere. 3–4 nodes/mm; 3–4 adapertural spines/mm; 3–4 adapical spines/mm. Apical wall not observed.

*Occurrences*.—Lower and Middle Devonian rocks of New York and Pennsylvania; localities 121, 124–126, 132–135, 142, 144, 232, 235–236, and 239. *Conularia continens*, here referred to *C. desiderata*, has been reported from Devonian rocks in Ohio (Claypole, 1903) and in Indochina (Patte, 1926), but the specimens upon which these references were based were not studied. Woodward (1943) identified *C. continens*

←

face. 7.3; AMNH CU 282G, same specimen as in Fig. 7.1, detail of major face. 7.4; CMNH 44584, ?major face of flattened specimen; locality 175. 7.5–7.9; *C. milwaukeeensis* Cleland. 7.5; USNM 85988, holotype; locality 255. 7.6; USNM 78212; detail of apical region. Note that no apical wall is present; locality 253. 7.7; MPM 20252, complete specimen; locality 253. 7.8; MPM 20252, same specimen as in Fig. 7.7, detail of major face. 7.9; MPM 22974; locality 253. Bar scales represent 1 cm.

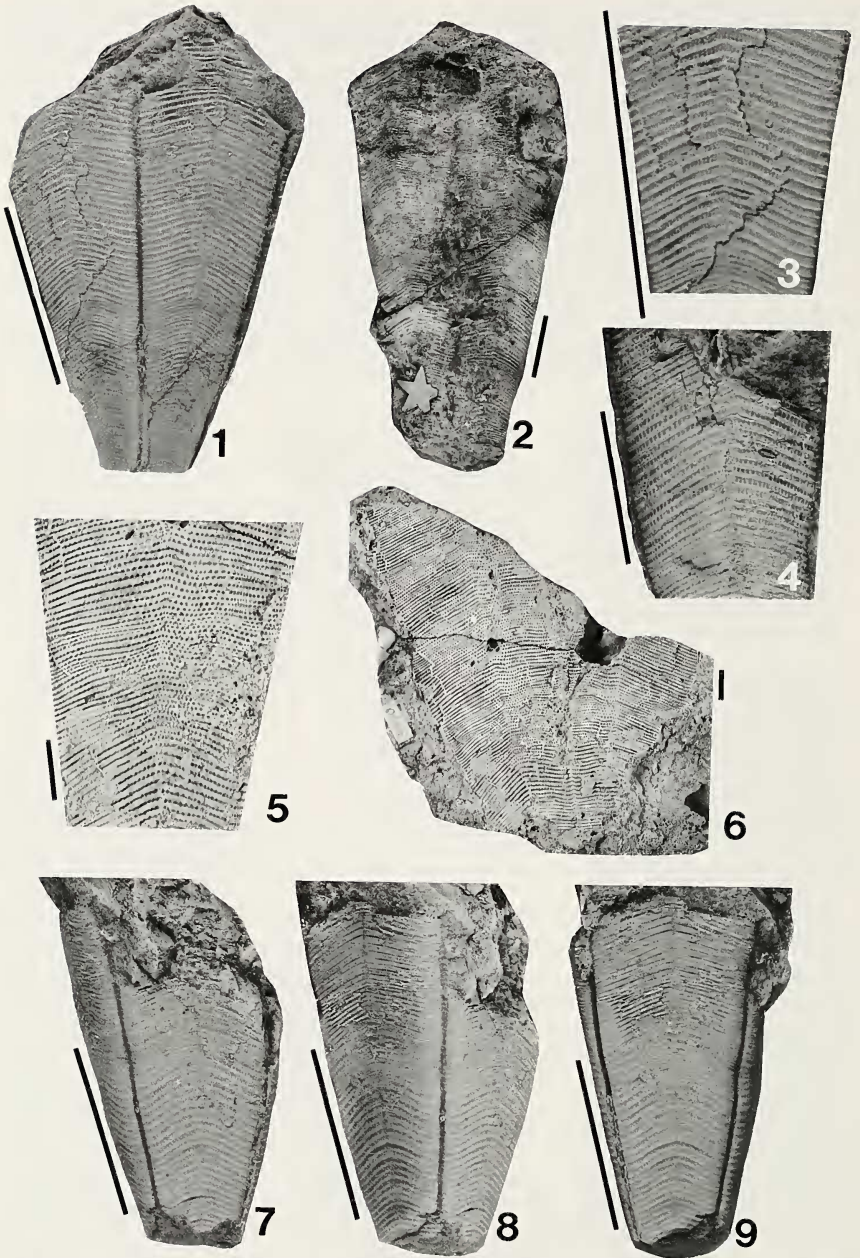


Fig. 8.—*Conularia pyramidalis* Hall. 8.1; AMNH 33017, lectotype; corner view of flattened specimen, preserved in calcareous shale; locality 117. 8.2; NYSM 3488, holotype of *C. huntiana* Hall, corner view, preserved in calcareous shale; locality 118. 8.3; AMNH

var. *rudis* (= *C. delphiensis*) in the Devonian of West Virginia, but Woodward's specimens were unavailable for study.

*Types.*—Holotype and plastoholotype of *C. delphiensis* Hall, AMNH 2697; two syntypes of *C. continens* Hall, NYSM 3485, NYSM 3486; holotype of *C. continens* var. *rudis* Hall, part and counterpart, NYSM 3487.

*Remarks.*—*Conularia desiderata* Hall is similar in appearance only to *C. pyramidalis* Hall. Both species have rod angles in the range of 14–27°. Also, specimens of both taxa possess rods which appear to be inflected at the midline. Features that are present in *C. desiderata*, but not present in *C. pyramidalis* include inflected circular curve to angulated circular curve rod articulation style and rod angles of 14–27°.

The syntypes of *C. continens* Hall differ morphologically from the holotype of *C. desiderata* Hall only in being flattened. The holotype of *C. continens* var. *rudis* differs from the holotype of *C. desiderata* in being larger and better preserved. The type specimens of each taxon have inflected gothic arch rod articulation in the region close to the apex and inflected circular curve rod articulation elsewhere. The major apical angle of the holotype of *C. desiderata*, measures 23°; the minor apical angle cannot be measured with certainty. The syntypes of *C. continens* have major apical angles of 16° and 19°. The major apical angle of the holotype of *C. continens* var. *rudis* is 27°. All of the type specimens have between 14 and 27 rods/cm and possess spines which are difficult to observe in most specimens. *Conularia continens* Hall and *C. continens* var. *rudis* Hall are, therefore, here considered junior synonyms of *C. desiderata* Hall.

*Material examined.*—48 specimens; housed in the AMNH, BMS, GSC, NJSM, NYSM, USNM and the private collections of Larry Decina and Paul Zell.

### **CONULARIA ELEGANTULA** Meek, 1871

Figs. 3.4, 7.1–7.4

*Conularia elegantula* Meek, 1871, p. 85–86; Meek, 1873, p. 228–229, Pl. 23, fig. 4; Miller, 1877, p. 141; Bigsby, 1878, p. 78; Whitfield, 1882, p. 242; Miller, 1889, p. 390; Babcock and Feldmann, 1986, fig. 2K.

*Conularia* s.l. *elegantula* Meek. Sinclair, 1948, p. 283.

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←  
33017, same specimen as in Fig. 8.1, detail of a minor face. 8.4; NYSM 3488, same specimen as in Fig. 8.2, detail of a minor face. 8.5; NYSM 3490, holotype of *C. lata* Hall, detail of major face; locality 122. 8.6; NYSM 3490, same specimen as in Fig. 8.5, entire specimen, preserved as an external mold in fine-grained sandstone. 8.7; AMNH 33018; paralectotype, preserved in three dimensions, major face; locality 117. 8.8; AMNH 33018, same specimen as in Fig. 8.7, corner view. 8.9; AMNH 33018, same specimen as in Fig. 8.7, minor face. Bar scales represent 1 cm.

*Description.*—Exoskeleton up to 7 cm in length. Major apical angle 20–30°; minor apical angle about 17°. Rod articulation uniformly of angulated circular curve style. 6 nodes/mm on rods. 6 adaperatural spines/mm; 6 adapical spines/mm. Rods usually abut at midline; approximately 40% alternate left superior on major and minor faces; rod angle 3–13°. 32–39 rods/cm. Apical wall not observed.

*Occurrences.*—Middle Devonian of Ohio; localities 174–176.

*Type.*—Holotype, AMNH CU 282G.

*Remarks.*—*Conularia elegantula* Meek is similar to *C. pyramidalis* Hall in the values for rod angles, the number of nodes/mm on the rods and in the number of spines/mm. *Conularia elegantula* can be distinguished from *C. pyramidalis*, and, indeed, all other species of *Conularia* from the Devonian or Mississippian of North America by its rod articulation architecture, which seems to be uniformly of angulated circular curve style. Partial specimens of *C. desiderata* exhibiting rods from the apertural region can also be distinguished from specimens of *C. elegantula* by the curvature of the rods as they approach the corner angles. The rods of specimens of *C. elegantula* are noticeably more inflected in the apertural direction than are rods belonging to specimens of *C. desiderata*.

*Material examined.*—Three specimens; housed in the AMNH and the CMNH.

### **CONULARIA MILWAUKEENSIS** Cleland, 1911

Figs. 7.5–7.9

*Conularia congregata* var. *milwaukeeensis* Cleland, 1911, p. 130, pl. 26, figs. 4–7; Teller, 1911, p. 251.

*Mesoconularia milwaukeeensis* (Cleland). Sinclair, 1948, p. 119.

*Conularia congregata milwaukeeensis* Cleland. Munthe, 1980, p. 6.

*Description.*—Exoskeleton up to 5 cm in length. Major apical angle 12–15°; minor apical angle 11–14°. Rod articulation uniformly of inflected gothic arch style. Rods abut at midline; rod angle 5–18°. 18–24 rods/cm. 5–7 nodes/mm; 5–7 adaperatural spines/mm; 5–7 adapical spines/mm. Apical walls not observed.

*Occurrence.*—Middle Devonian of Wisconsin; localities 253–255.

*Types.*—Holotype, USNM 85988; five paratypes, USNM 78212. Two paratypes, listed by Sinclair (1948) as MPM 244–245, could not be found.

*Remarks.*—*Conularia milwaukeeensis* may be distinguished from similar appearing species such as *C. elegantula* Meek and *C. desiderata* Hall by having only inflected gothic arch style rod articulation and by attaining lengths of up to 5 cm, apparently without the addition of apical walls. *Conularia elegantula* has narrow apical angles like *C. milwaukeeensis*, but its rod articulation style is exclusively angulated circular curve. Likewise, *C. desiderata* has narrow apical angles, but

its rod articulation patterns include inflected circular curve style in the apical region and angulated circular curve style elsewhere.

None of the examined specimens of *C. milwaukeeensis* preserves integument over the entire exoskeleton. Because of this, rods have obviously been moved slightly from their original positions, making the measurement of rod angles difficult. Also, because of the general lack of preserved integument in most specimens, there is no evidence that apical walls were developed in this species. Apical walls may have been a feature of this species, but simply have not been preserved in the samples studied.

*Material examined.*—37 specimens; housed in the GSC, MPM, and the USNM.

### **CONULARIA MULTICOSTATA** Meek and Worthen, 1865

Figs. 9.1–9.5, 9.8, 10.1, 10.4, 12.1–12.5

*Conularia multicostata* Meek and Worthen, 1865, p. 252–253; Bigsby, 1878, p. 316; Miller, 1889, p. 390; Weller, 1898, p. 190; Babcock and Feldmann, 1986, figs. 1A, 1F.

*Conularia micronema* Meek, 1871, p. 84; Meek, 1875, p. 316, Pl. 18, figs. 1a–d; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Herrick, 1888a, p. 94–95, Pl. 2, figs. 18–19; Herrick, 1888b, p. 49, Pl. 8, figs. 4–4a; Lesley, 1889, p. xv; Miller, 1889, p. 390, fig. 643; Herrick, 1893, Pl. 19, figs. 4–4a; Weller, 1898, p. 190; Grabau and Shimer, 1910, p. 13, figs. 1227c–f.

*Mesoconularia multicostata* (Meek and Worthen). Sinclair, 1948, p. 125.

*Mesoconularia micronema* (Meek). Sinclair, 1948, p. 124.

*Mesoconularia mcfarlani* Sinclair, [1948], p. 126–128, Pl. 16, figs. 3–5.

*Mesoconularia attica* Sinclair, [1948], p. 125–126, Pl. 9, fig. 2, Pl. 17, figs. 9–11.

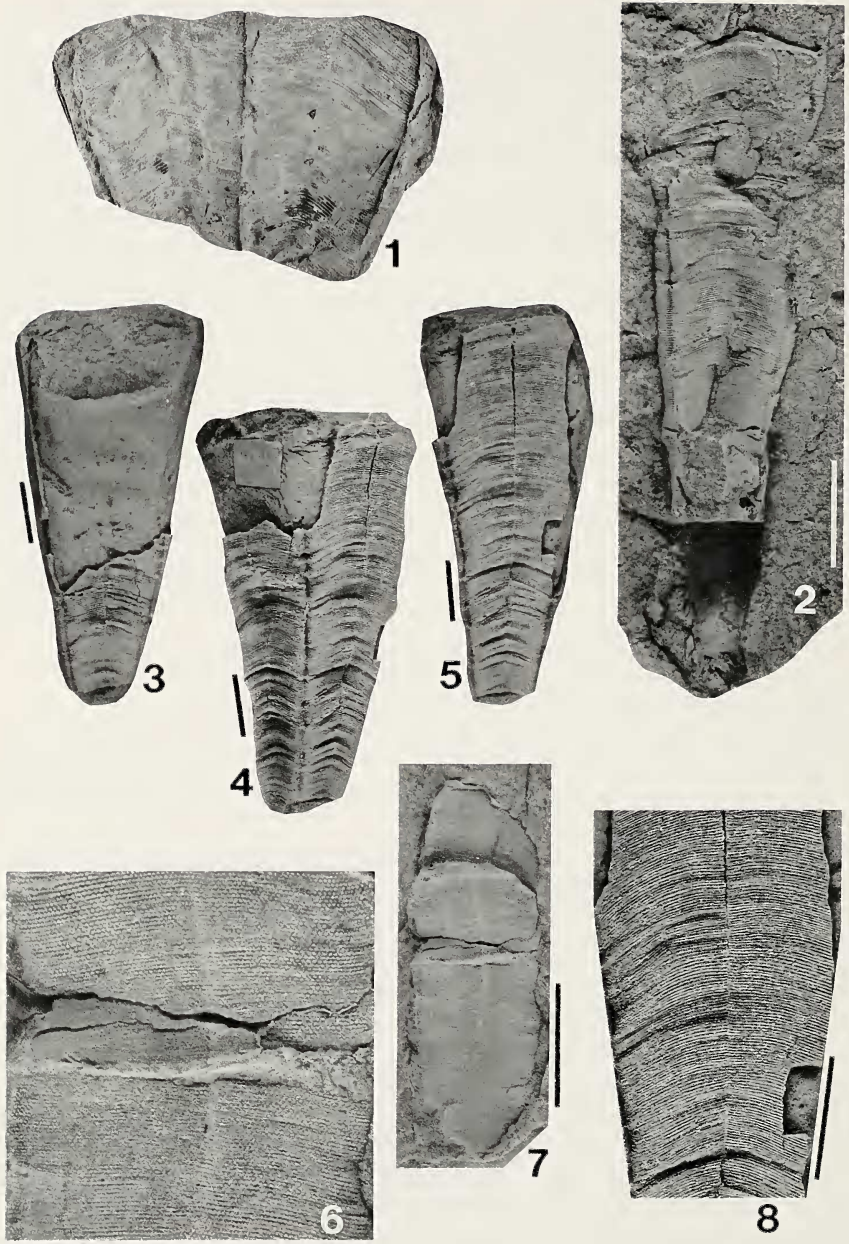
*Diconularia micronema* (Meek). Sinclair, 1952, p. 138–139; Moore and Harrington, 1956b, p. F61, fig. 47.2.

*Non Conularia trentonensis multicosta* Ruedemann, 1912, p. 115–116; Ruedemann, 1930, p. 36; Goldring, 1935, p. 63.

*Description.*—Exoskeleton up to 25 cm in length. Major apical angle 20–24°; minor apical angle 18–22°. Rod articulation of inflected gothic arch style in apical and most other regions and of angulated circular curve style in apertural region of large specimens; rods exhibiting inflected circular curve style articulation are mildly recurved near the midline but they are angulated in the apertural direction at the midline. Rods abut at midline; rod angle 9–17°. 26–60 rods/cm. Nodes prominent; 2–3 nodes/mm; 2–3 ad-apertural spines/mm; 2–3 adapical spines/mm. Apical wall not observed.

*Occurrences.*—Lower Mississippian of Indiana, Kentucky and Ohio; localities 25, 71–73, 79–80, 193, 197–200, 205, 209, 214, 217–218, 223, 225, 227 and 228.

*Types.*—Holotype of *Conularia multicostata* Meek and Worthen is lost; plastoholotype, with small fragments of fossil adhering, USNM 50157. Holotype of *C. micronema* Meek is apparently lost (Sinclair, 1948, p. 124); neotype, AMNH 6713. Specimen intended by Sinclair (1948) to be holotype of *Mesoconularia mcfarlani*, UK 6089. Three



specimens which Sinclair (1948) intended to designate as types of *M. attica*, CM 34533-34534, GSC 87204.

*Remarks.*—*Conularia multicosata* Meek and Worthen is most similar in morphology to *C. subcarbonaria* Meek and Worthen. Like *C. subcarbonaria*, *C. multicosata* has prominent nodes and can have more than 30 rods/cm. However, *C. multicosata* can be distinguished from this and all other species of *Conularia* by the combination of its very closely spaced rods, 26–60/cm, and its inflected gothic arch rod articulation in most places except the apertural region of large specimens. More importantly, though, the rods of specimens referred to *C. subcarbonaria* appear to be undulose. This is especially true for large individuals (for example, Figs. 11.2–11.3).

In the apertural region of specimens of *C. multicosata* which are large for the species, a unique form of angulated circular curve rod articulation is present. This rod articulation pattern involves slight recurvature beginning about  $\frac{1}{2}$  to  $\frac{1}{3}$  of the distance between the midline and the corner angle; at the midline, the rods are slightly angulated. Approximately 70% of specimens of *C. multicosata* are found to have well developed exoskeletal constrictions (for example, Figs. 9.3–9.5, 9.8, 10.1). These cannot be used as a species-level or genus-level taxonomic criterion, however, since well preserved exoskeletal constrictions have been observed in specimens belonging to nearly every taxon reported herein and in Part B. This species is notable because it shows good examples of this structure more frequently than any other known species of conulariid from the Devonian or Mississippian of North America.

According to Meek and Worthen (1865, p. 253), *C. multicosata* is unique among conulariids in that it possesses rods so closely spaced that “it is only under a good magnifier that the very minute crenulations can be seen.” Later, Meek (1871, p. 84) described *C. micronema* as a

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Fig. 9.—9.1–9.5; *Conularia multicosata* Meek and Worthen. 9.1; USNM 50157, plasto-holotype. Dark areas on photograph indicate areas where integument of the original specimen still adheres; locality 203. 9.2; UK 6089, specimen intended by Sinclair (1948) to be the holotype of *Mesoconularia mcfarlani* Sinclair, preserved in siderite concretion; probably minor face; locality 73. 9.3; AMNH 6713, specimen chosen by Sinclair (1942*b*) as neotype of *C. micronema* Meek, major face; locality 225. 9.4; AMNH 6713, same specimen as in Fig. 9.3, corner view. 9.5; AMNH 6713, same specimen as in Fig. 9.3, minor face. 9.6–9.7; *C. subcarbonaria* Meek and Worthen. 9.6; FMNH UC 6610, holotype of *C. intertexta* Miller; detailed view of exoskeleton, locality 28. 9.7; FMNH UC 6610, same specimen as in Fig. 9.6, view of entire specimen. 9.8; *C. multicosata* Meek and Worthen, AMNH 6713, same specimen as in Fig. 9.3, detailed view of minor face. Bar scales represent 1 cm.

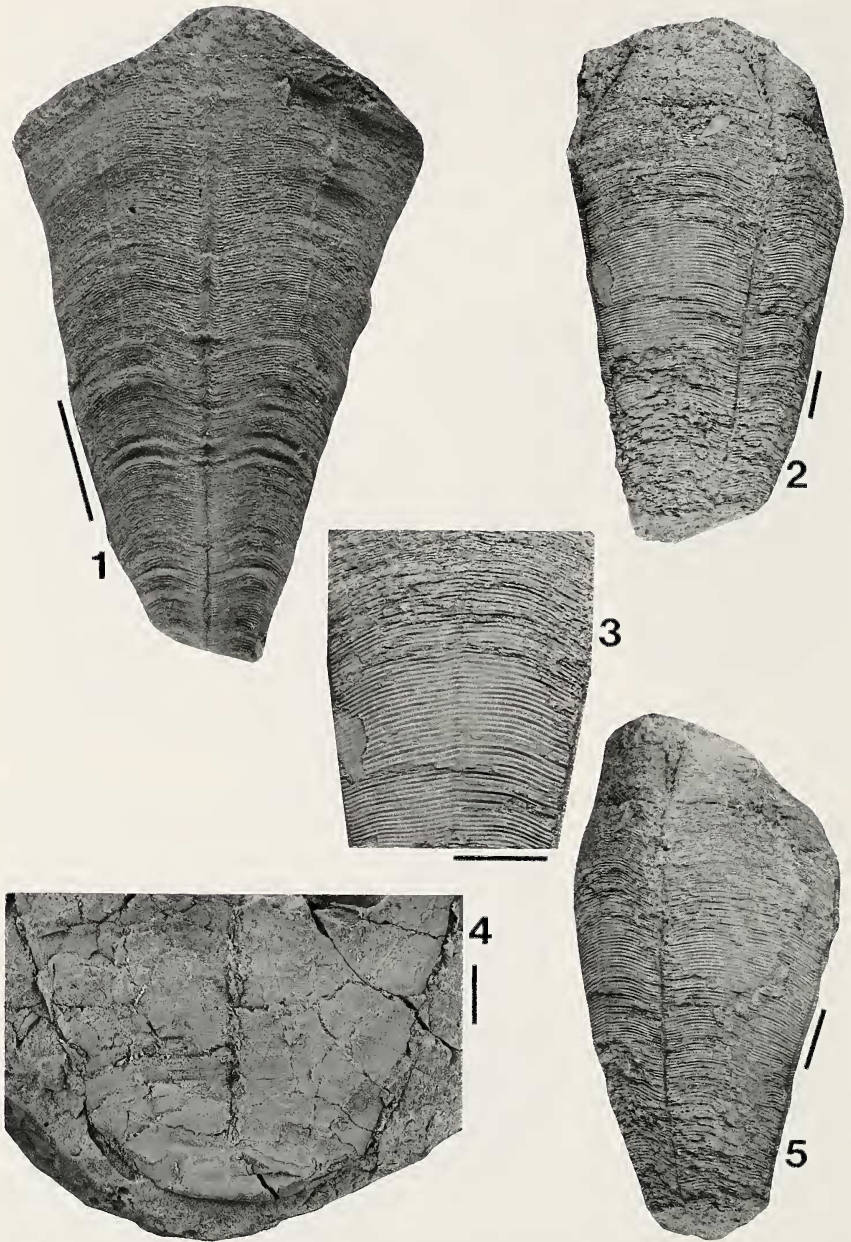


Fig. 10.—10.1–10.3; *Conularia multicostata* Meek and Worthen, 10.1; USNM 50128, corner view of specimen with pronounced exoskeletal constrictions; locality 225. 10.2–



conulariid distinct from all others because it possessed rods so closely spaced that "it requires the aid of a magnifier to see them distinctly." In all morphological respects, the two species are remarkably similar, assuming that AMNH 6713 is "typical" of the species *C. micronema* as suggested by Sinclair (1948, p. 142). *Conularia micronema* Meek is here considered a junior synonym of *C. multicosata* Meek and Worthen.

Two manuscript species, *Mesoconularia mcfarlani* Sinclair and *M. attica* Sinclair, are here placed in synonymy with *C. multicosata* for the reason that they have very closely spaced rods and nodes. Values for spacing of the rods and nodes are consistent with other specimens referred to *C. multicosata* (see Appendix B in part B). The specimen which Sinclair intended to designate the holotype of *M. mcfarlani* (Fig. 9.2) possesses an angulated circular curve style of rod articulation and is very similar in morphology to specimens from the Mississippian of Ohio which have been referred herein to *C. multicosata*. The same can be said for the three specimens (CM 34533–34534, GSC 87204) referred to as *M. attica* in Sinclair's (1948) unpublished thesis.

*Conularia micronema* was used by Sinclair (1952, p. 138) as the type species of the genus *Diconularia*. Sinclair (1952, p. 138–139) noted that *Diconularia* was a probable form-genus which differs from *Conularia* in routinely having closely spaced rods and an "accentuation of the pustules." *Conularia*, by contrast, was judged by Sinclair to exhibit these features only in gerontic specimens. The genus *Diconularia* is here included as a junior subjective synonym of *Conularia* because there does not appear to be any consistent pattern of differences between "*D.*" *micronema* and species included by Sinclair in the genus *Conularia*. Examples supporting this argument are given below.

*Conularia niagarensis* Hall, the North American reference species for the genus *Conularia* (Sinclair, 1940a), has large, well-pronounced nodes and rod spacing values in the range of about 12–24/cm. These characters closely resemble those of the "typical" specimen of "*D.*" *micronema*, AMNH 6713 (see Appendix B in Part B). The number of rods/cm exhibited in AMNH 6713, 28–32, is well within the limits of the genus *Conularia* as recognized herein. Species referable to *Conu-*

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10.3; *C. subcarbonaria* Meek and Worthen. 10.2; UIPC 10680, holotype, minor face, preserved in limestone; locality 13. 10.3; UIPC 10680, same specimen as in Fig. 10.2, detail of minor face. 10.4; *C. multicosata* Miller and Gurley, USNM 50647, apical region of specimen showing apical wall; locality 228. 10.5; *C. subcarbonaria* Meek and Worthen, UIPC 10680, same specimen as in Fig. 10.2, major face. Bar scales represent 1 cm.

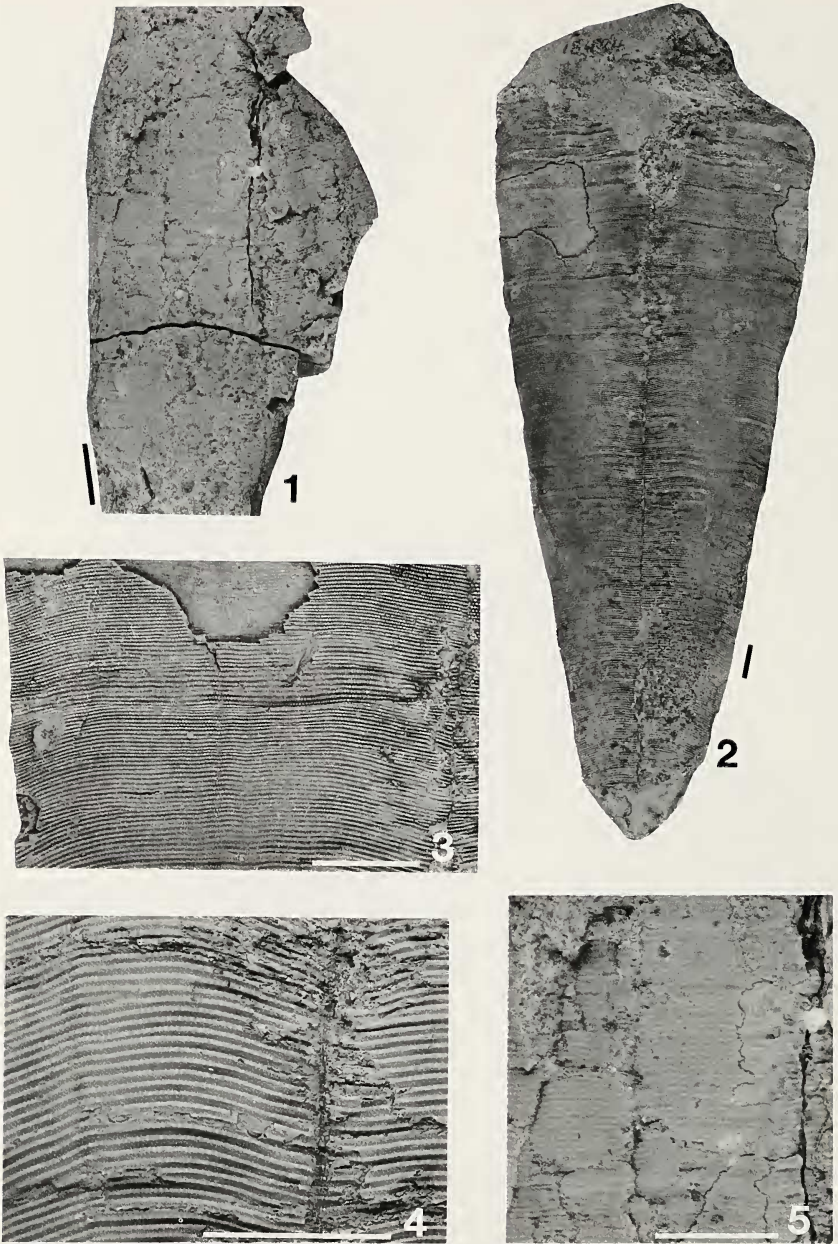


Fig. 11.—*Conularia subcarbonaria* Meek and Worthen. 11.1; FMNH UC 6289, badly weathered holotype of *C. spergenensis* Miller and Gurley, preserved in limestone; locality

*laria* from the Devonian and Mississippian of North America exhibit 9 to 84 rods/cm. Furthermore, no species of *Conularia* examined from Devonian or Mississippian age rocks of North America are known to consistently possess rods which are more closely spaced in large, presumably gerontic, individuals than in "average-sized" individuals.

*Material examined.*—67 specimens; housed in the AMNH, CM, CMNH, FMNH, GSC, and the USNM and the private collection of Ron Fisher.

### **CONULARIA PYRAMIDALIS** Hall, 1859

Figs. 3.3, 8.1–8.9, 16.7

*Conularia pyramidalis* Hall, 1859, p. 347–348; Hall, 1861, Pl. 72A, figs. 1a–c; Miller, 1877, p. 141; Miller, 1889, p. 390; Whitfield and Hovey, 1899, p. 170–171; Richardson, 1942, p. 23–26, Pl. 3, figs. 4–9; Sinclair, 1948, p. 106; Babcock and Feldmann, 1986, fig. 2E.

*Conularia huntiana* Hall, 1859, p. 348; Hall, 1861, Pl. 72A, figs. 2a–b; Clarke and Ruedemann, 1903, p. 566; Grabau, 1906, p. 151, fig. 65; Grabau and Shimer, 1910, p. 13, fig. 1224; Sinclair, 1948, p. 106, Pl. 9, fig. 1.

*Conularia lata* Hall, 1859, p. 479–480, Pl. 70A, fig. 3, Pl. 91, fig. 1; Bigsby, 1878, p. 78; Miller, 1889, p. 390; Sinclair, 1948, p. 104.

*Conularia huntana (sic)* Hall, Miller, 1877, p. 141; Miller, 1889, p. 390.

*Description.*—Exoskeleton up to 20 cm in length. Major apical angle 17–23°; minor apical angle 16–17°. Rod articulation gothic arch style in apical region and inflected gothic arch elsewhere. Rods abut at midline; rod angle 5–22°. 7–17 rods/cm. 1–4 nodes/mm; 1–4 adaperatural spines/mm; 1–4 adapical spines/mm. Apical wall not observed.

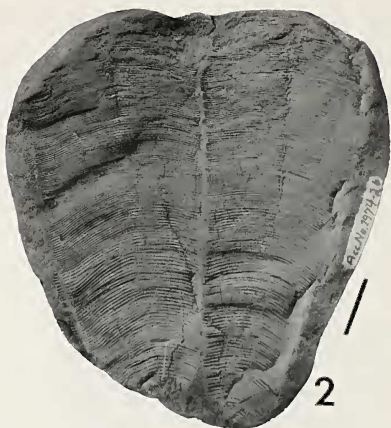
*Occurrences.*—Lower Devonian of New Jersey and New York; localities 114, 116–120 and 122.

*Types.*—Lectotype, designated herein from James Hall's syntypic suite of four specimens, AMNH 33018, smaller of two specimens bearing this number (Figs. 3.3, 8.1, 8.3); three paratypes, AMNH 33018, larger specimen, and AMNH 33019, two specimens. Holotype of *C. huntiana* Hall, NYSM 3488; holotype of *C. lata*, NYSM 3490, plas-toholotype, GSC unnumbered.

*Remarks.*—*Conularia pyramidalis* Hall is similar in size and apical angles to *C. desiderata* Hall. Distinction between the two taxa is made on the basis of differences in rod angles, 9–14° for *C. pyramidalis* versus 13–17° for *C. desiderata*. Additionally, when complete enough speci-

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44. 11.2; FMNH UC 18494, larger of two specimens, flattened specimen with apical wall preserved, preserved in calcareous shale; locality 38. 11.3; FMNH UC 18494, same specimen as in Fig. 11.2, detail of major face. Note apparent convergence of rods at exoskeletal constriction. 11.4; UIPC 10680, same specimen as in Fig. 10.2, detail in region of corner groove; locality. 11.5; FMNH UC 6289, same specimen as in Figure 11.1, detail of exoskeleton. Bar scales represent 1 cm.



mens are studied, distinction between these two species can be made on the basis of rod articulation style, gothic arch to inflected gothic arch for *C. pyramidalis*, compared to gothic arch to inflected circular curve for *C. desiderata*. Differences in rod articulation styles immediately serve to help distinguish *C. pyramidalis* Hall from *C. undulata* Conrad, though both may attain lengths greater than 15 cm. *Conularia pyramidalis* Hall is readily distinguished from *C. elegantula* Meek by having significantly fewer nodes and spines per unit space than are present in *C. pyramidalis*. The feature which immediately serves to distinguish *C. pyramidalis* from *C. multicostata* Meek and Worthen is the greater spacing between rods, 9–14/cm in *C. pyramidalis* and up to 32/cm in *C. multicostata*. *Conularia multicostata* and *C. subcarbonaria* Meek and Worthen have more prominent nodes on the rods than does *C. pyramidalis*.

*Conularia huntiana* Hall was distinguished from *C. pyramidalis* Hall (Hall, 1859, p. 348) by its greater length, its smaller apical angles, the greater convexity of its faces and differences in the appearance of ridges and spines. The apical angles of the lectotype of *C. pyramidalis* are 18° and 16°, and in the holotype of *C. huntiana*, the apical angles as measured are 13° and 11°. However, the holotype of *C. huntiana* is not compressed to the extent that the lectotype of *C. pyramidalis* is. Moreover, the lectotype of *C. pyramidalis* is a smaller specimen and presumably represents an earlier growth interval than does the holotype of *C. huntiana*. Therefore, a smaller set of apical angles is expected in *C. huntiana*. Differences in convexity of the faces between the two taxa is likely a result of differences in collapse of the exoskeletons after death of the animals and/or differences in compression of the exoskeletons. Differences in the appearance of the ridges and spines seem to be functions of preservation: most of the lectotype of *C. pyramidalis* is preserved as an internal mold, whereas the holotype of *C. huntiana* retains much integument. Where integument is present on the lectotype of *C. pyramidalis*, it is identical to that on the holotype of *C. huntiana* (compare Figs. 8.3 and 8.4). In both specimens, most of the rods are broken out, leaving a “double ridge” arrangement of the integument,

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Fig. 12.—*Conularia multicostata* Meek and Worthen. 12.1; GSC 87204, enlargement of a specimen intended by Sinclair (1948) to be a paratype of *Mesoconularia attica*; locality 193. 12.2; CMNH 4684, external mold of a flattened specimen preserved in a siderite concretion; locality 198. 12.3; CM 34533, specimen intended by Sinclair (1948) to be the holotype of *M. attica*; locality 193. Note that the apical wall is present. 12.4; FMNH UC 54014A, specimen figured by Herrick (1888a) as *C. micronema*; locality 228. 12.5; GSC 87204, same specimen as in Fig. 12.1, view of a collapsed specimen preserved in a siderite concretion; locality 193. Bar scales represent 1 cm.

marking the former positions of the margins of the rods within the integument.

*Conularia lata* Hall is included as a junior subjective synonym of *C. pyramidalis* largely because of qualitative similarities including nearly identical rod articulation styles. Also, values for apical angles and rod spacing are similar in the lectotype of *C. pyramidalis* and the sole specimen referred to *C. lata* by Hall, NYSM 3490. Major and minor apical angles for the lectotype of *C. pyramidalis* are 18° and 17°, respectively. For the holotype of *C. lata*, they are 23° and 17°. Rods/cm values for the lectotype of *C. pyramidalis* vary between 9 and 14 while those of the holotype of *C. lata* vary between 7 and 10. Values for rod angles and node spacing on the rods for both specimens are also well within the expected normal distribution for a species.

*Material examined.*—41 specimens; housed in the AMNH, CM, CMNH, FMNH, GSC, NJSM, NYSM, USNM, and the private collection of Paul Zell.

### **CONULARIA SUBCARBONARIA** Meek and Worthen, 1865

Figs. 9.6–9.7, 10.2–10.3, 10.5, 11.1–11.5

*Conularia subcarbonaria* Meek and Worthen, 1865, p. 253; Meek and Worthen, 1873, p. 520–522, Pl. 19, figs. 4a–c; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Miller, 1889, p. 390; Keyes, 1894, p. 218; Weller, 1898, p. 191–192.

*Conularia intertexta* Miller (*nomen nudum*), 1892*b*, p. 692.

*Conularia intertexta* Miller, 1894, p. 317, Pl. 10, fig. 4; Weller, 1898, p. 190.

*Conularia spergenensis* Miller and Gurley, 1893, p. 74–75, Pl. 8, fig. 2; Miller, 1897, p. 765; Weller, 1898, p. 191.

*Mesoconularia subcarbonaria* (Meek and Worthen). Sinclair, 1948, p. 123.

*Mesoconularia intertexta* (Miller). Sinclair, 1948, p. 123.

*Diconularia micronema* (Meek). *Sensu* Lane, 1973, p. 92–93, Pl. 8, figs. 2–3.

*Description.*—Exoskeleton up to 35 cm in length. Major apical angle 10–21°; minor apical angle 9–19°. Rods are undulose; rod articulation uniformly of angulated circular curve style. Rods abut at midline; rod angle 4–6°. 17–31 rods/cm. Nodes prominent; 3–5 nodes/mm on rods; no spines present. Apical wall may be present.

*Occurrences.*—Upper Devonian–Lower Mississippian of Illinois, Indiana, Iowa and Missouri; localities 8–9, 13, 20, 24, 27–28, 37–38, 42, 44–46, 48, 51, 61, 64, 67, and 101.

*Types.*—Holotype, UIPC 10680, plastoholotypes USNM 50158, FMNH UC unnumbered and GSC unnumbered. Holotype of *C. intertexta*, FMNH UC 6610, plastoholotypes, USNM 68130 and GSC unnumbered; holotype of *C. spergenensis*, FMNH UC 6289.

*Remarks.*—In the possession of prominent nodes along the rods, *C. subcarbonaria* Meek and Worthen resembles the Mississippian species, *C. multicostata* Meek and Worthen, and the Devonian species, *C. ulsterensis* Howell. These taxa are readily distinguished, however, on the basis of rod articulation style: *C. subcarbonaria* possesses angulated

circular curve rod articulation in which the rods are undulose, particularly in large individuals. On the other hand, *C. multicostata* has both angulated circular curve and inflected gothic arch rod articulation and *C. ulsterensis* possesses only inflected gothic arch rod articulation. Additionally, *C. ulsterensis* is unique among the species of *Conularia* studied in having a rod spacing of 45–84 rods/cm in adult specimens.

Like the Devonian species, *C. undulata* Conrad, *C. subcarbonaria* possesses undulose rods. *Conularia subcarbonaria* can be distinguished from *C. undulata* in having more prominent nodes along the rods and by having rods which nearly always abut at the midline. The rods of *C. undulata* alternate at the midline in approximately 10% of the cases studied.

*Conularia intertexta* Miller is considered synonymous with *C. subcarbonaria* because of general qualitative similarities between the types of the two species and because of similarities in the value for number of rods/cm (see Appendix B in Part B). However, the holotype specimen (Figs. 9.6–9.7) of *C. intertexta* is very badly preserved, making any species-level assignment somewhat doubtful. One characteristic of the specimen is an apparently undulose set of rods. It is primarily because of its undulose rods that *C. intertexta* is here included in synonymy with *C. subcarbonaria*.

The holotype of *C. spergenensis* Miller and Gurley (Figs. 11.1, 11.5) is, like the holotype of *C. intertexta*, badly preserved. However, like the holotype of the latter taxon, *C. spergenensis* bears qualitative and quantitative similarities to *C. subcarbonaria*, most notably, undulose rods. It too is therefore considered to be a junior subjective synonym of *C. subcarbonaria*.

*Material examined.*—46 specimens; housed in the AMNH, FMNH, GSC, ISGS, IUPC, and the USNM.

### *CONULARIA TUZOI* Clarke, 1907

Fig. 15.3

*Conularia desiderata* var. *tuzoi* Clarke, 1907, p. 181, fig.; Clarke, 1908, p. 144, Pl. 11, fig. 13; Dresser and Denis, 1944, p. 326.

*Conularia tuzoi* Clarke. Sinclair, 1948, p. 105.

*Description.*—Description based only upon holotype. Exoskeleton 11.3 cm in length. Major apical angle approximately 10°; minor apical angle not observed. Rod articulation style unknown in vicinity of apex and of inflected gothic arch style elsewhere; rods are broadly inflected. Rods abut at midline; rod angle 9–10°. Nodes and spines not observed. Apical wall not observed.

*Type.*—Holotype, NYSM 9404.

*Occurrence.*—Lower Mississippian of Quebec; locality 244.

*Remarks.*—The holotype of *C. tuzoi* (Clarke) is badly preserved and no additional specimens are known. A cross sectional view is not pre-

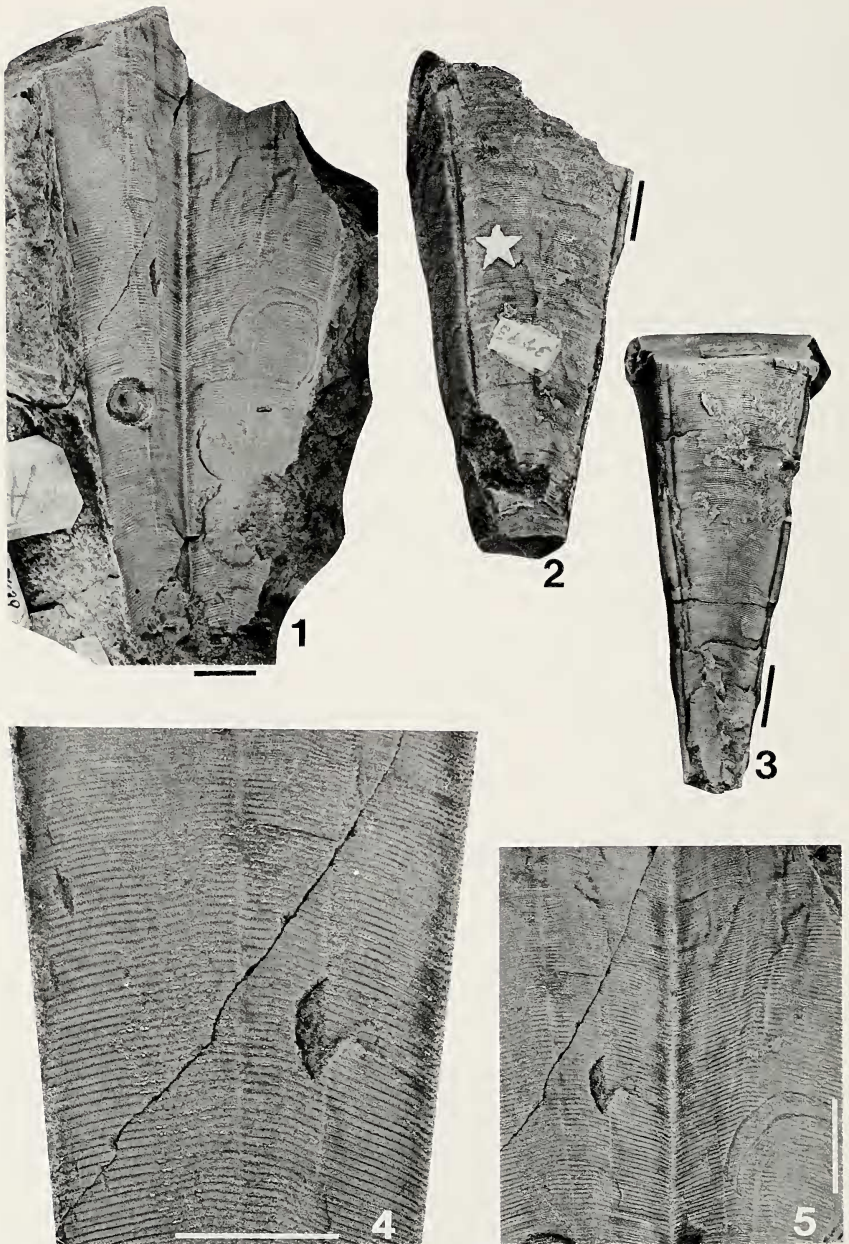


Fig. 13.—*Conularia undulata* Conrad. 13.1; AMNH 41093, neotype, preserved as an external mold in siltstone. Note rounded marks produced by orbiculoid brachiopods



served on the holotype. This taxon appears to differ from other species of *Conularia* included in this paper in the possession of broadly rounded inflections where the rods are of inflected gothic arch style.

*Material examined.*—1 specimen, NYSM 9404.

**CONULARIA ULSTERENSIS** Howell, 1942

Figs. 15.4, 16.1–16.3, 16.5

*Conularia ulsterensis* Howell, 1942, p. 91, figs. 10–11; Goldring, 1943, p. 208.

*Mesoconularia ulsterensis* (Howell). Sinclair, 1948, p. 117.

*Description.*—Exoskeleton up to 3 cm in length. Major apical angle 14–19°; minor apical angle 10–15°. Rod articulation uniformly of inflected gothic arch style. Rods usually abut at midline; rod angle 11–15°. 45–84 rods/cm. Nodes prominent; 6–8 nodes/mm; 6–8 adapertural spines/mm; 6–8 adapical spines/mm. Apical wall not observed.

*Types.*—Holotype, PU 42071; two paratypes, PU 42072–42073.

*Occurrences.*—Lower Devonian of New York and Pennsylvania; localities 115, 231, 234 and 236. Specimens possibly referable to this taxon have also been found in the Lower Devonian of Quebec; locality 242.

*Remarks.*—This species is distinct in its possession of up to 84 rods/cm in adult specimens, the largest number recorded in the genus *Conularia*. It can also be distinguished by its prominent, closely spaced nodes. In this form, nodes are spaced as closely as 7/mm. Some specimens of *C. undulata* Conrad may have as many as 7 nodes/mm, but *C. undulata* has neither inflected gothic arch rod articulation throughout the exoskeleton nor prominent nodes.

The specimen of *C. ulsterensis* Howell illustrated in Fig. 16.2 is preserved as an internal mold. It is unusual in that it clearly shows that a longitudinal invagination existed along the integument internal to the midline.

*Material examined.*—7 specimens; housed in the CM, NJSM, and the NYSM.

**CONULARIA UNDULATA** Conrad, 1841

Figs. 13.1–13.5, 14.1–14.5, 15.1–15.2, 16.4

*Conularia undulata* Conrad, 1841, p. 57; Hall, 1861, p. 62–63; Bigsby, 1878, p. 62–63; Hall, 1876, Pl. 29, figs. 1–7; Hall, 1879, p. 208–209, Pl. 33, figs. 1–5, 7; Pl. 34A, figs. 1–4; Miller, 1889, p. 390; Whitfield and Hovey, 1901, p. 326–327; Grabau,

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that were previously attached to the conulariid exoskeleton; locality 145. 13.2; NYSM 3493, preserved in siltstone, major face; locality 145. 13.3; NYSM 3494, preserved in siltstone, major face; locality 145. 13.4; AMNH 41093, same specimen as in Fig. 13.1, detail of major face. 13.5; AMNH 41093, same specimen as in Fig. 13.4, detail in region of corner groove. Bar scales represent 1 cm.

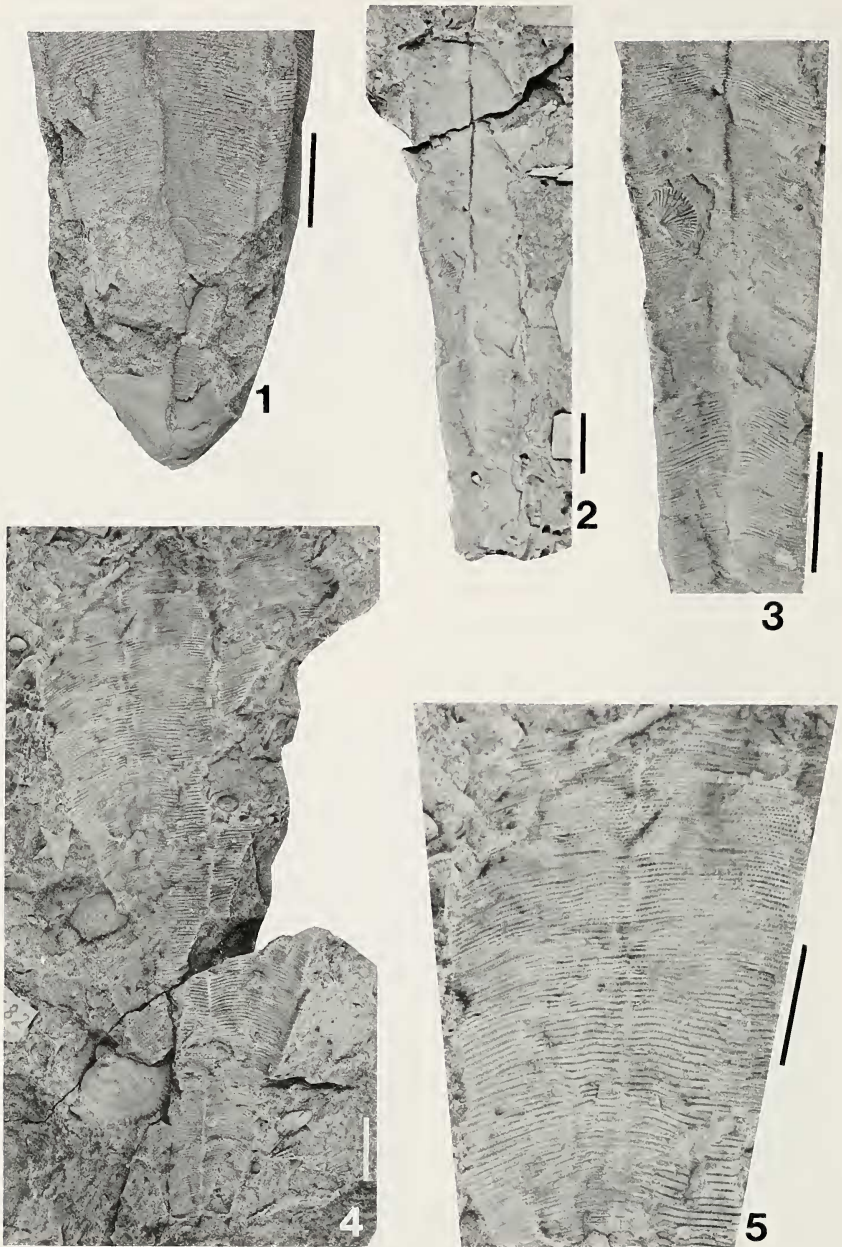


Fig. 14.—*Conularia undulata*. 14.1; AMNH 5439, specimen showing relation of apical wall to the remainder of the exoskeleton. Note flange for connection at adapertural end

- 1899, p. 284–285, fig. 219; Grabau and Shimer, 1910, p. 13, fig. 1225–1226; Moore and Harrington, 1956b, p. F60, fig. 25.2; Babcock and Feldmann, 1986, fig. 21.
- Conularia cayuga* Hall, 1876, Pl. 28, figs. 2–3; Hall, 1879, p. 211–212, Pl. 34, figs. 2, 5; Miller, 1889, p. 390.
- Conularia crebistria* Hall, 1876, Pl. 29, figs. 8, 9.
- Conularia crebistriata* (sic) Hall, 1879, p. 210–211, Pl. 33, figs. 8–9, Pl. 34A, fig. 5; Miller, 1889, p. 390; Moore and Harrington, 1956b, p. F60, fig. 42.9.
- Mesoconularia undulata* (Conrad). Sinclair, 1948, p. 118.
- Conularia* s.l. *cayuga* Hall. Sinclair, 1948, p. 285.
- Ctenoconularia crebistriata* (sic) (Hall). Sinclair, 1948, p. 241, Pl. 6, figs. 10–11.
- Ctenoconularia crebistria* (Hall). Sinclair, 1952, p. 142.
- Conularia* sp. cf. *C. undulata* Conrad. Kasznica, 1986, p. 14–15, fig. 2.

*Description.*—Exoskeleton up to 15 cm in length. Major apical angle 10–18°; minor apical angle 8–15°. Rod articulation uniformly of inflected circular curve style; rods are undulose in the apertural ½. Rods usually abut at midline; rod angle 10–18° in apical region and 4–20° elsewhere. 17–32 rods/cm. 4 nodes/mm; 4 adapertural spines/mm; 4 adapical spines/mm. Apical wall may be present.

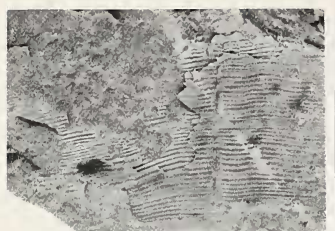
*Types.*—Neotype, AMNH 41093, plastoneotype, FMNH UC 694; James Hall's figured specimens, NYSM 3493, 3494, AMNH 5439. Holotype of *C. crebistria*, AMNH 5440, plastoholotype, FMNH UC 679; holotype of *C. cayuga*, NYSM 3482, plastoholotype, FMNH UC 685.

*Occurrences.*—Middle Devonian of Maine, Maryland, New York, Ontario, Pennsylvania, and Quebec; localities 90–91, 115, 128–129, 136–138, 140–141, 143, 145–148, 230, 236–238, and 241. Ulrich (1892) has indicated that *C. undulata* is present in the Devonian of Bolivia and Reed (1904) has cited this taxon in the Devonian of South Africa. These identifications are erroneous, and are described briefly below. They will also be described in greater detail elsewhere. Cordini (1955, p. 275, fig. 81) referred and figured some fossils found in Antarctica as *C.* cf. *C. undulata*, but these have been subsequently identified as plant remains (Dalziel et al., 1981).

*Remarks.*—Conrad's suite of syntypes is lost. However, judging from his description of *C. undulata* (Conrad, 1841, p. 57) it is clear that the species is based upon specimens now referable to either *C. undulata* or *C. pyramidalis* Hall. Hall's early figures and description of *C. undulata* (Hall, 1876, Plate 29, figs. 1–7, explanation of Plate 29; 1879, p. 208–209; Plate 33, figs. 1–5, 7, Plate 34A, figs. 1–4) have served as bases for all subsequent studies on the species. Therefore, it is appro-

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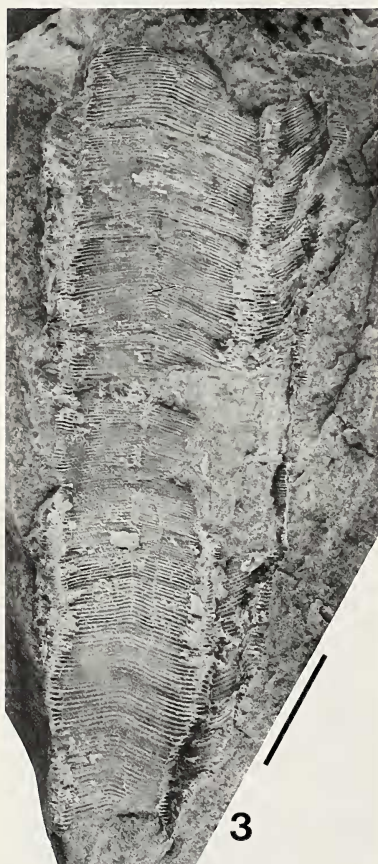
of apical wall; locality 145. 14.2; AMNH 5440, holotype of *C. crebistria* Hall, preserved in calcareous shale, minor face; locality 136. 14.3; AMNH 5440, same specimen as in Fig. 14.2, detail of minor face. 14.4; NYSM 3482; holotype of *C. cayuga* Hall, preserved in calcareous shale; locality 136. 14.5; NYSM 3482, same specimen as in Fig. 14.4, detailed view of minor face. Bar scales represent 1 cm.



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Fig. 15.—15.1–15.2; *Conularia* cf. *C. undulata* Conrad. 15.1; NYSM 9410, detail of exoskeleton; locality 241. 15.2; NYSM 9408, flattened and tectonically distorted specimen; locality 90. 15.3; *C. tuzoi* Clarke, NYSM 9404, holotype; locality 244. 15.4; NYSM

priate to select a neotype from among Hall's extant specimens. The specimen chosen, AMNH 41093, is the subject of one of the best known of Hall's figures of the taxon.

Two Devonian species are here considered junior subjective synonyms of *C. undulata* Conrad: *C. cayuga* Hall and *C. crebistria* Hall. *Conularia crebistria*, according to Hall (1879, p. 210) differed from *C. undulata* in being "more slender in its mode of growth" and in having more closely spaced rods. In terms of the arrangement of nodes and spines, the two were judged to be "precisely similar." The holotype of *C. crebistria*, AMNH 5440, is a badly preserved specimen exhibiting one face (Figs. 13.2–13.3). The apical angle cannot be determined because the specimen has been distorted and the corner grooves are not preserved on the surface of the slab. Like specimens of *C. undulata*, this specimen has inflected circular curve rod articulation. The rods are undulose in the vicinity of the aperture. The holotype of *C. crebistria* has rod spacing values ranging from 24 to 30 rods/cm and node spacing values of about 4 nodes/mm. No other values can be determined with confidence from this specimen. The equivalent values for the lectotype of *C. undulata* are 20–27 rods/cm and 6 nodes/mm. There seems to be no significant difference in the features exhibited in AMNH 5440 from other specimens here referred to *C. undulata*.

The holotype of *C. cayuga*, NYSM 3482, is a flattened specimen preserved as an external mold (Figs. 13.4–13.5). An apical wall is present. Hall (1879, p. 211–212) indicated that, in general, this specimen is "not dissimilar to *C. undulata*." However, subtle differences, including "stronger" rods, wider spaced rods except in the apertural region and the presence of "striae" between adjacent rods (=spines) were used as key characters which served to distinguish this taxon from *C. undulata*. Spines, of course, are present in *C. undulata*, just as they are in the holotype of *C. cayuga*. The rods of NYSM 3482 have a spacing of 17–22/cm, well within the expected range of values for individuals of *C. undulata*. Other quantitative determinants, given in Appendix B in Part B, substantiate this conclusion. The rods are undulose except near the apical wall and are articulated in angulated circular curve style, similar to the neotype of *C. undulata*. The rods do not appear to be better pronounced than those shown in specimens referred to *C. undulata* which are preserved as external molds, including the neotype (Fig. 13.4). Thus, the holotype of *C. cayuga* is here referred to Conrad's species, *C. undulata*.

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9411, *C. ulsterensis* Howell, two specimens, one preserving an apical wall; locality 242. Bar scales represent 1 cm.

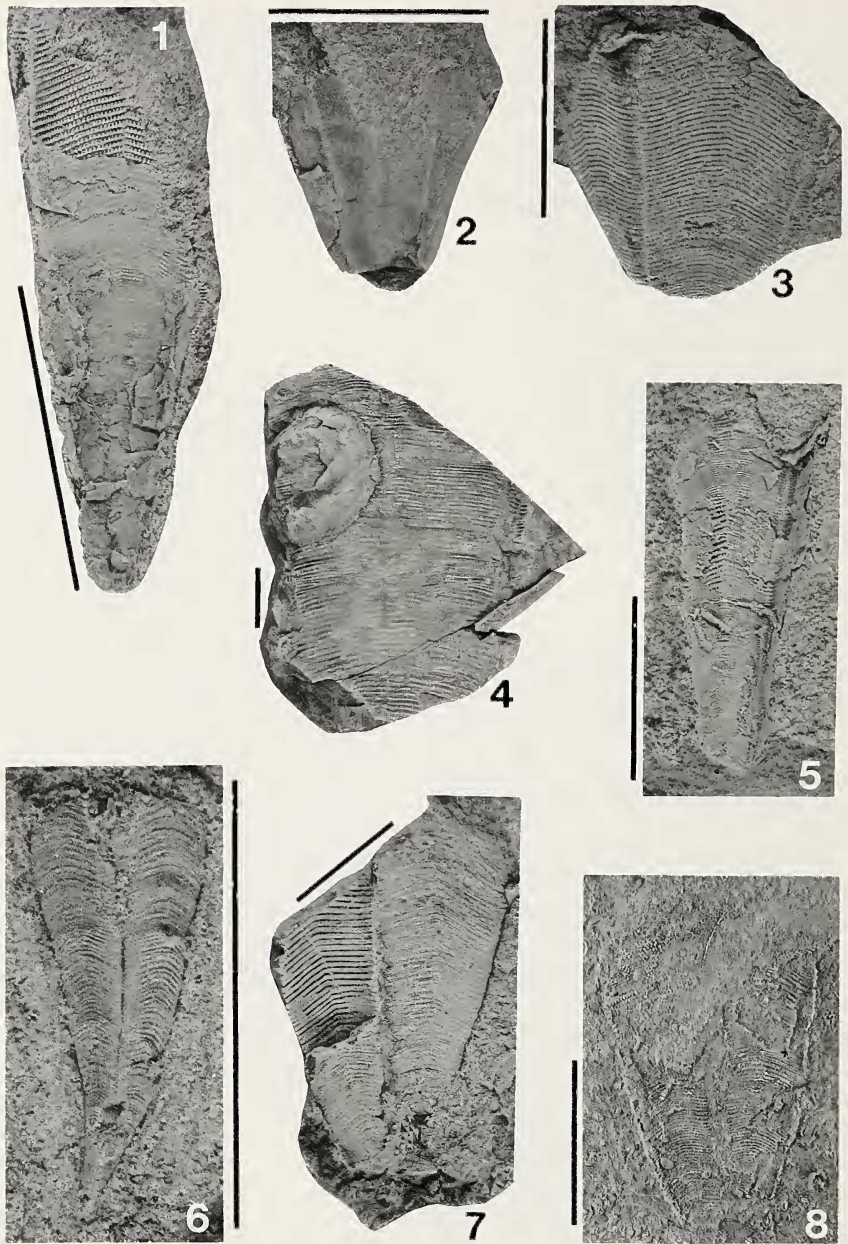


Fig. 16.—16.1–16.3; *Conularia ulsterensis* Howell. 16.1; PU 42071, holotype; locality 115. 16.2; PU 42072, paratype; internal mold showing longitudinal ridges at the midlines; locality 115. 16.3; NJSM 12843, external mold; locality 236. 16.4; CM 34520, *C. un-*

Sinclair (1948, p. 118) and Sinclair and Richardson (1954, p. 105) stated that the species *C. grandis* Roemer is synonymous with *C. undulata*. However, this cannot be substantiated here because the specimen upon which Roemer's description is based (Roemer, 1856, p. 436, Plate 3, figs. 21a–b) was not available for study. It is likely that the holotype of *C. grandis* is lost.

*Conularia undulata* is similar to *C. subcarbonaria* Meek and Worthen in the possession of an undulose mode of angulated circular curve style rod articulation. It differs from the latter form in having nodes on the rods which are not prominent. Moreover, the rods of *C. subcarbonaria* nearly always abut at the midline. In *C. undulata*, as many as 10% of the rods may alternate at the midline.

Two specimens from the Devonian of the Malvinokaffric Realm have been misidentified as *C. undulata*. The first (Ulrich, 1892, p. 31–33, Pl. 3, figs. 6a–b), which was collected in Bolivia, is referable to *C. albertensis* Reed, judging from Ulrich's well-executed figure. *Conularia albertensis* differs from *C. undulata* in having gothic arch rod articulation in the apical region and inflected gothic arch rod articulation elsewhere, whereas *C. undulata* has only inflected circular curve rod articulation. The second specimen from the Malvinokaffric Realm which was misidentified as *C. undulata* was described and figured by Reed (1904, p. 248–249, Pl. 31, figs. 1–1a). It was collected from the Bokkeveld beds of South Africa. A latex mold (UCGM 34720) of the specimen has been examined. It is referable to *C. quichua* Ulrich. *Conularia quichua* and *C. undulata* both have undulose rods, but *C. quichua* has rods articulated in gothic arch fashion in the apical region and in angulated circular curve style elsewhere.

*Material examined*.—43 specimens housed in the AMNH, CM, FMNH, GSC, NYSM, NJSM, USNM, and the private collections of Gordon Baird, Robert Linsley and Paul Zell.

### CONULARIA sp.

Fig. 16.8

*Conularia* cf. *huntiana* Hall. Merriam, 1973, p. 35, Pl. 12, figs. 18–20.

*Occurrence*.—Upper Devonian of Nevada; Locality 108.

*Remarks*.—Remains of at least six conulariid specimens from the Devonian of Nevada were figured and described by Merriam (1973,

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*dulata* Conrad, portion of specimen with orbiculoid brachiopod attached; locality 91. 16.5; *C. ulsterensis* Howell, CM 34528. 16.6; *C. desiderata* Hall, USNM 395827, juvenile, with apex intact; locality 142. 16.7; *C.* cf. *C. pyramidalis* Hall, GSC 2598; locality 241. 16.8; *C.* sp., USNM 159536; locality 108. Bar scales represent 1 cm.

p. 35, Plate 12, figs. 18–20). Merriam identified these specimens as *C. cf. huntiana*. The specimens (USNM 159536), one of which is figured herein (Fig. 16.8), are poorly preserved and cannot be assigned to a species at present.

The specimens in question possess an inflected circular curve rod articulation. The rods are slightly deflected adaperturally at the midline. This style of rod articulation is similar to that observed in specimens of *C. desiderata* Hall.

*Material examined.*—6 specimens; housed in the USNM.

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